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7

FIRE SURVIVAL AND LIFE HISTORIES OF ACACIA AND DICHROSTACHYS SPECIES IN A SOUTH AFRICAN SAVANNA

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TABLE OF CONTENTS

SUMMARY	5
ACKNOWLEDGEMENTS	8
1 INTRODUCTION: THE EFFECT OF FIRE ON SAVANNA TREES	9
1.1 Fire in savannas	9
1.2 Biological Effects of fire	10
1.3 Grass-tree coexistence	13
1.4 Theory in practice	14
1.5 Aim of this study	17
1.6 Thesis structure	17
1.7 Study area and species	20
1.8 References	22
2 THE RESPROUTING BIOLOGY OF FOUR WIDESPREAD TREE SPECIES IN THE HLUHLUWE-UMFOLOZI PARK	28
2.1 Introduction	28
2.2 Response of savanna trees to fire	28
2.3 Aim of this study	31
2.4 Methods	31
2.4.1 Study Area	31
2.4.2 Experimental Approach	32
2.4.3 Clipping treatments	32
2.4.4 Pre-clip and regrowth measurements recorded	33
2.4.5 Seedling response to clipping	35
2.5 Results	35
2.5.1 Variation in resprouting ability	35
2.5.1.1 General characteristics	35
2.5.1.2 Height dependent survival	37
2.5.1.2.1 Patterns of mortality across height classes	37
2.5.1.2.2 Effects of different clipping treatments	37
2.5.1.3 Location and size of bud banks	37
2.5.1.3.1 Variation in origin of resprouting stems across species, clipping treatments and height classes	37

2.5.1.3.2	Variation in number of resprouting stems across species, clipping treatments and height classes	42
2.5.2	Variation in resprouting vigour	45
2.5.2.1	Height recovery	45
2.5.2.2	Rates of stem self-thinning	49
2.5.2.3	Sum of the length of all resprouting stems	50
2.5.2.4	Response of trees to clipping at a low versus high rainfall sites	55
2.6	Discussion	55
2.6.1	Resprouting ability	55
2.6.1.1	Height dependent survival	55
2.6.1.2	Location of buds and size of bud banks	56
2.6.2	Resprouting vigour - The ecological implications of different resprouting strategies	58
2.6.2.1	Height recovery	58
2.6.2.2	Rates of self thinning in resprouting stems	60
2.7	Conclusion	63
2.8	References	64
3	RESPONSE OF <i>ACACIA KARROO</i> , <i>ACACIA NILOTICA</i> AND <i>DICHROSTACHYS CINEREA</i> TO FIRE	66
3.1	Introduction	66
3.2	Aim of this study	68
3.3	Methods	68
3.3.1	Study Area	68
3.3.2	Fire intensity measurement	69
3.3.2.1	Estimating fuel load	69
3.3.2.2	Fuel moisture content	70
3.3.3	Tree response following fire	70
3.3.4	Bark thickness	71
3.3.5	Data analysis	71
3.4	Results	72
3.4.1	Fire intensity measurements	72
3.4.2	Tree response	73
3.4.2.1	Species abundance	73
3.4.2.2	Tree mortality	77
3.4.2.3	Topkill rates	78
3.4.2.4	Regrowth rates	83
3.4.3	Bark thickness	93
3.5	Discussion	95
3.5.1	Fire intensity measurements	95
3.5.2	Tree response	95
3.5.2.1	Species abundances	95
3.5.2.2	Patterns of mortality	95

3.5.2.3	Patterns of topkill	96
3.5.2.4	Regrowth rates	98
3.5.3	Bark thickness	99
3.6	Conclusion	100
3.7	References	101
4	TREE RESPONSE TO VARIATION IN SEASON OF DEFOLIATION	103
4.1	Introduction	103
4.2	Aim of the study	105
4.3	Methods	106
4.3.1	Study area	106
4.3.2	Study species	106
4.3.3	Experimental design	106
4.3.4	Data analysis	107
4.3.5	Root carbohydrate reserves	108
4.4	Results	108
4.4.1	Regrowth variables	108
4.4.1.1	Regrowth height	108
4.4.1.2	Number of resprouting stems	114
4.4.1.3	Sum of the length of resprouting stems	116
4.4.2	Phenology	119
4.4.3	Starch analysis	119
4.5	Discussion	122
4.6	Conclusion	125
4.7	References	127
5	GULLIVERS: A DISTINCTIVE LIFE HISTORY STAGE IN SAVANNA TREES	129
5.1	Introduction	129
5.2	Demography of gullivers	131
5.3	The morphology of gullivers	136
5.4	Life history evolution in gullivers	139
5.5	Discussion	141
5.6	References	144

6	CONCLUSIONS AND MANAGEMENT IMPLICATIONS	147
6.1	Key research findings	147
6.2	Management recommendations	149
6.3	Recommendations for future research	152
6.4	Conclusion	154
6.5	References	155
	APPENDIX A	156
	LOCATION AND PHYSICAL INFORMATION FOR EACH STUDY SITE	156
	APPENDIX B	158
	TAXONOMY AND BOTANICAL DESCRIPTIONS OF THE FOUR STUDY SPECIES	158
	References	162

SUMMARY

The tree-grass mix defines savannas, yet savannas can be defined as ecosystems that move between transition states of grass and bush, the dynamics of which are complex, being affected by a number of biotic and abiotic factors. Recently there has been renewed interest in fire and its role in shaping and maintaining savanna communities in Africa. Other than its ability to radically alter the savanna components, relatively little is known about the mechanistic effects of fire regimes on the structural and functional dynamics of the ecosystem. Furthermore, the biological basis of the observed response has been very poorly studied. An improved understanding of savanna tree biology and how they respond to disturbance is essential for more effective ecosystem management.

This study investigates variation in response of savanna trees to fire, and the underlying causes, in the Hluhluwe-Umfolozi Park, KwaZulu Natal, South Africa. This variation is explored by means of clipping experiments and controlled burns, across species, tree height (seedlings to adults), a rainfall gradient, and intensity and season of injury. The four study species were *Acacia karroo*, *A. nilotica*, *A. caffra* and *Dichrostachys cinerea*. A total of 670 trees were subjected to different clipping treatments and their response monitored for two years. The response of 1512 trees was assessed following eight controlled burns of varying intensity and season. I investigated seasonal variation in root starch storage as a possible mechanisms underlying tree response.

I found that trees exhibited marked differences in response to injury, within and between species, from arid to mesic sites and across different fire seasons. Both resprouting ability and vigour were assessed. All four study species had the ability to resprout at a very early age (i.e. at 6 months) and this ability was retained and improved with tree height, until maturity when sprouting ability rapidly declined. *Acacia caffra* adults were an exception in that trees retained resprouting ability through to adulthood. Resprouting vigour is critical for predicting the frequency of escape opportunities of injured or topkilled trees and this was found to vary within and among species, following a similar size dependent pattern.

Trees also responded differently following injury in summer versus winter. Summer burns killed substantial numbers of *A. nilotica* and *D. cinerea*, but not *A. karroo*. Mortality was

higher after summer burns than in the "normal" winter burns in the dormant growth season. I investigated the seasonal variation in root starch storage as a possible mechanism underlying this response and found that the Acacias, especially *A.karoo*, had relatively high starch concentration in their roots relative to *D.cinerea*. The species with the lowest root starch concentrations (*D.cinerea*), responded most to injury in the growing season. Species with large root starch concentrations were relatively unaffected.

Differences in starch concentration and season of burn response correspond with life history differences among the three species. *D.cinerea* grows to maturity almost entirely within the zone of maximum fire damage, typically suffers 100% topkill, and probably uses post-burn photosynthate to recover canopy area. *A.karoo* and *A.nilotica* both grow to maturity only after emerging to heights where the canopy is not destroyed by burning. To do so, they appear to require substantial root carbon reserves to build long enough stems between successive fires to escape topkill. *D.cinerea*, with no need to build tall stems, most likely relies on the current year's photosynthesis for recovery from injury. *A.nilotica*'s strategy differs slightly to *A.karoo* in having a slower regrowth rate, however, it eventually manages to escape the flame zone by having much thicker bark than *A.karoo* and *D.cinerea*, and can withstand topkill to a greater degree.

Two distinct life histories, gulliver and non-gulliver, are developed to distinguish the species in this study. Gullivers are the juvenile phase of savanna trees which are prevented from escaping to become adults by frequent injury from burning. Trees may spend a greater part of their lives in this stunted state than as tall adult trees. The characteristic feature of gullivers is a marked discontinuity in growth and reproductive patterns above and below the critical height at which trees escape topkill. *A.nilotica* and *A.karoo* display typical gulliver type life histories where juveniles start as multi-stemmed and eventually emerge from the fire zone as single stemmed trees. Adults lose their sprouting ability. The non-gulliver type species, *A.caffra* and *D.cinerea*, survive to maturity within the flame zone, and remain multi-stemmed throughout. *A.caffra* retains vigorous sprouting ability when mature whereas *D.cinerea* loses this ability.

A simple model is used to explore the conditions under which gulliver type recruitment is favoured over precocious reproduction in the fire zone. Gulliver type life histories are expected to occur mainly in mesic savannas which are subjected to frequent fires. In arid

savannas, populations may be limited more by years of sufficient rainfall to produce seeds or allow successful seedling establishment. Cohorts of plants are more likely to date from unusual rainfall in arid savannas, and unusually long intervals between fires in mesic savannas.

The limitations of this study, implications for management and questions for future research are discussed.

University of Cape Town

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1 INTRODUCTION: THE EFFECT OF FIRE ON SAVANNA TREES

“.... the origin and preservation of grasslands are due, in the main to burning and,they are in fact great and, in some cases, ancient cultural practices....” (Sauer 1950).

1.1 Fire in savannas

Savannas are defined very broadly as tropical or near tropical seasonal vegetation with a continuous, often grass-dominated herbaceous layer and, in most cases but not necessarily, a significant but discontinuous layer of woody species (Frost *et al.* 1986). They cover 40% of South Africa (Menaut 1983; Trollope 1984) and 20-30% world's land surface (Scholes 1997; Scholes and Archer 1997). The grass layer has a high C4 component. Grass fires have occurred frequently throughout their evolutionary history and have been a major factor in the development of savannas over geological time. Some savannas have been derived recently through repeated burning by people (Feely 1980; Hopkins 1983). Rainfall, soil type, herbivory, fire and nutrients are considered to be the major determinants of savanna vegetation structure (Skarpe 1992; Scholes and Walker 1993; Frost 1996; Williams *et al.* 1996). However, of these, the impacts of fire and herbivory, particularly in the African savannas, are believed to be chiefly responsible for vegetation structure and for maintaining savanna-forest boundaries. Frequent fires are a feature of savannas worldwide and their effect on the tree component is the central theme of this thesis.

All savannas burn, and this is dependent on rainfall to produce enough fuel during summer. In mesic savannas fires occurs every 1-5 years (Frost and Robertson 1985). Today, fires are mostly anthropogenically induced and lit in the dry season, but lightning was also a major cause of fires in the past, and this has been well documented in southern Africa and in other parts of the world. Today lightning accounts for fewer fires than anthropogenically induced fires in savanna areas of South Africa mainly in the wet season (Manry and Knight 1986; Trollope 1993; van Wilgen *et al.* 1998).

Fire has probably been a feature in the African landscape since at least the Miocene (Kanthack 1907; Thompson 1936; Ellery and Mentis 1992; Bond and van Wilgen 1996). In

southern Africa, humans have used fire for more than 1.5 million years (Brain and Sillen 1988). Early Portuguese explorers noted that the interior of South Africa, from the Cape to Natal, was covered by plumes of smoke due to veld burning (Kanthack 1907; Thompson 1936) and subsequently gave the name "Terra dos Fumos" to the land. Other authors claim that veld burning was common practice long before the arrival of Europeans (Roux 1969). Fire was used widely to provide green and nutritious grazing for their livestock, and Bushmen of the Cape are said to have used fire in the same way to attract game for hunting. Honey hunters frequently started fires which spread across the landscape. In West African savannas Monnier (1968) suggests that fire is responsible for the maintenance of wet savanna at latitudes where climatic conditions favour rainforest. In fire exclusion experiments, fire has been shown to prevent tree invasion (e.g. Trollope 1993; Swaine *et al.* 1992; O'Connor 1985; O'Connor and Bredenkamp 1997).

1.2 Biological Effects of fire

Both the grass and woody component in savannas are well equipped to recover after fire, mostly by resprouting vegetatively. Grasses regenerate vigourously from seed or vegetatively (Lacey *et al.* 1982). The effects of fire on the grass composition, biomass and production has been the focus of extensive research due to their importance for livestock production. In comparison, the effect of fire on the tree layer is less well researched. The capacity for regeneration is well developed in most savanna trees (Lacey 1974; Lacey *et al.* 1982; Williams *et al.* 1999). Most savanna tree species survive fire by either having thick insulating bark amongst other features and or by resprouting from different regions on the root crown or stem. Once established, many tree species (e.g. many Acacias) can persist for decades, surviving repeated fires and browsing until there is a long enough fire free interval to grow above the flame height and escape defoliation by fire (Lacey *et al.* 1982). This may explain the bimodal size structure (i.e. canopy trees and juveniles) often observed in savanna tree populations (Braithwaite and Estbergs 1985). Several factors affect recovery in savanna trees including the size and age of the tree, and the intensity, season and frequency of defoliation.

Variation in fire intensity may influence tree mortality and tree architecture with the response often being size (height) dependent (Trollope *et al.* 1995). Resprouting ability is generally thought to increase with stem size (e.g. Wright *et al.* 1976; Moreno and Oechel

1991) but, in some tree species, decreases again in larger trees (Trollope 1974; Hodgkinson 1998). Fire induced mortality in savanna trees is very rare (Lacey 1974; Frost 1984; Hodgkinson 1998; Williams *et al.* 1999). Fire induced mortality acts most strongly on seedlings (Menaut *et al.* 1990), but Hodgkinson (1998) has shown that rates of mortality are highest in both seedlings and adults in some Australian savanna tree species. Some trees sprout from root suckers, others from the stem base or from the canopy. However, the basis for inter and intraspecific variation is poorly understood and may involve factors such as the location of buds, bark form (e.g. degree of fissuring) and thickness, and tree architecture. Tree response to fire season may vary depending on the state of carbon reserves at the time of the fire, the length of the growing season subsequent to burning or possibly just the interaction between season and fire intensity (i.e. largely determined by fuel load and moisture content). Lastly, different growth rates in different species and across different sized individuals may further define fire response strategies.

The importance of population processes in the tree component of savannas in limiting closed canopy formation is explored by Bond and Van Wilgen (1996) and Higgins *et al.* (2000). Bond and van Wilgen (1996) proposed a distinct life history, the “gulliver”, which is typically a multi-stemmed juvenile tree that remains trapped in the grass layer by fire fuelling grasses. It is thought that trees in this stage may persist longer than as adults. Taller, thicker stems and stems with thicker bark have a higher chance of surviving a fire of a given intensity (Wright *et al.* 1976; Moreno and Oechel 1991; Gignoux *et al.* 1997; Trollope *et al.* 1995). Therefore the chance of gullivers escaping to become adults, depends strongly on stem growth rates and the frequency and intensity of fire (Trollope 1984). However, precisely how fire influences the transition from seedling to adult stage in frequently disturbed systems requires further research attention. This is a key step in bush encroachment which is not adequately understood.

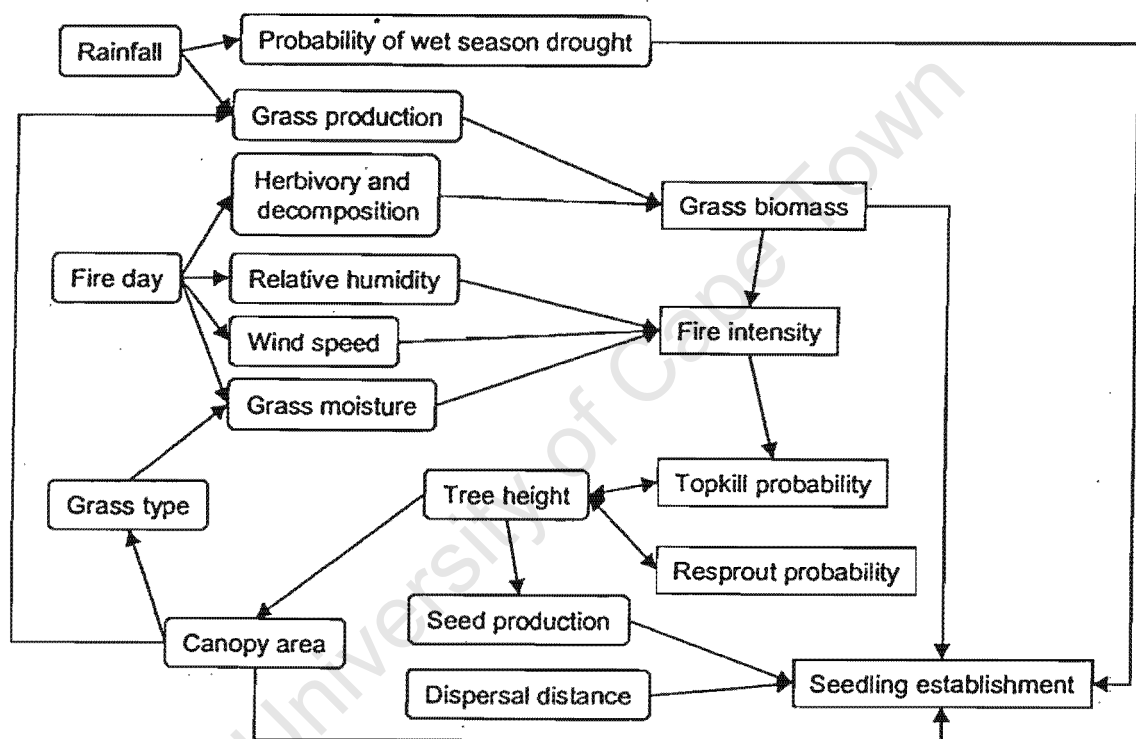


Figure 1.1 Conceptual model of grass-tree interaction developed by Higgins *et al.* (2000). The model shows the factors that influence seedling establishment, fire intensity and the probability of stem mortality.

1.3 Grass-tree coexistence

What determines the grass-tree mix in savannas? Why are tree seedlings not eliminated by grasses through competition and fire? Or conversely, why are grasses not excluded by trees? These are some of the questions that have kept savanna ecologists intrigued for the past few decades. Answers to these questions are of importance for ecological theory on savannas and thus of relevance for their management whether for subsistence or commercial scale farming, and for wildlife-reserve management. Several theories have been proposed to explain grass-tree coexistence in savannas including rooting niche separation (Walter 1971; Walker and Noy-Meir 1982; Knoop and Walker 1985). These theories have been reviewed in detail elsewhere (Belsky 1990; Scholes 1997; Scholes and Archer 1997; Higgins *et al.* 2000).

Fires are more intense and frequent in wet savannas relative to dry savannas due the higher fuel loads produced. In wet savannas it is expected that fire is more important in controlling grass-tree interactions (Frost *et al.* 1986), although the mechanism for this is not well understood. Higgins *et al.* (2000) suggest that understanding how grass and trees coexist requires a clearer understanding of several factors; grass fire behavior, fire induced tree damage, tree recruitment and seedling establishment. They developed a model for grass-tree interaction, demonstrating that coexistence is possible for a range of environmental conditions (Figure 1.1). The novel features of this model are that it is the first to incorporate tree life history variation in growth and resprouting response which are considered the key factors in understanding savanna ecosystem dynamics and management. Variation in tree recruitment is dependent not only on variation in the fire regime (i.e. frequency, intensity and season) but also on tree life history. Savanna trees only recruit into the adult population once they escape the zone of influence of grass fires. The potent resprouting ability of topkilled (i.e. above ground parts killed by fire) trees is a key life-history trait that promotes the persistence of trees in savanna (Walter 1971; Trollope *et al.* 1995; Bond and van Wilgen 1996; Gignoux *et al.* 1997). Trees within the flame zone may persist as suppressed juveniles (called "gullivers" by Bond and van Wilgen 1996) for many years resprouting after numerous fires (Trollope 1998).

Optimal management of savannas will depend increasingly on a sound knowledge of the different savanna ecosystems, their structure and dynamics. Savanna ecology lags behind the substantial and rapidly improving body of knowledge in temperate systems. In comparison with tropical grasslands, our knowledge of savanna functioning is poor, particularly the population ecology of the woody component and its interaction with fire and browsers. Skarpe (1991) suggests this may be due to a bias towards applied research and lack of support for basic research. As a result, there is little generally applicable knowledge, while local surveys and inventories are plentiful. The lack of information on plant population ecology and savanna ecosystem dynamics and succession hamper our ability to manage savanna rangelands effectively.

Apart from the pastoral focus, in southern Africa much savanna research has been aimed at the control of encroaching tree species, in the past and more recently. However there is no clear understanding of how species differ in response. Previous research has contributed significantly to our understanding of savanna dynamics at the systems level, an approach that has dominated research and management in South African savannas (Scholes and Walker 1993). However, we know a great deal less about the population biology of savanna trees. I believe that, with only limited understanding of the ecology and biology of tree life histories, management recommendations are often based on pure speculation, and negligible testing of models on which the speculation is based.

1.4 Theory in practice

Managing the balance of trees and grass is the central management concern in savannas throughout the world. Savannas exhibit a high degree of variation in structure from open grassland to closed woodland. However, an increasing tendency to woodiness has been widely documented in savannas across the globe (e.g. Africa (Kelly and Walker 1976; van Vegten 1983; Frost *et al.* 1986; Le Roux 1996), Australia (Harrington *et al.* 1984), and North and South America (Buffington and Herbel 1965; Blackburn and Tueller 1970; Smeins 1983; Archer *et al.* 1988)). Today dense woody thickets characterize vast areas of the earth's grasslands and savannas. This phenomenon is widely referred to as "bush encroachment" in southern Africa. However the meaning of this term is somewhat controversial among researchers, some believing it is ambiguous. In South Africa, bush encroachment means both the large scale conversion of former grassland vegetation to

a savanna physiognomy by encroaching indigenous trees, as well as the increase in size and density of woody plants within historical savanna areas (Le Roux 1996). In this thesis the term bush encroachment is used in this broad sense.

Bush encroachment is often described as a successional sequence where small-leaved leguminous woody species, often Acacias, initiate the process. These are often followed by broad-leaved woody species (Le Roux 1996) which tend to form closed-canopy woodland. Le Roux (1996) developed a conceptual model of the dynamics of bush encroachment in South Africa, which appears similar to that developed for the southern Texas savannas by Archer *et al.* (1988). The rate of encroachment can be rapid. Quantitative assessments have shown that many wooded areas seen today were once grassland or open savanna. In African savannas the increase in woody plant cover has occurred over the last 50-300 years (Kelly and Walker 1976; van Vegten 1983; Watson 1995). Irvine (1943) documented a shift from open grassland to bush encroachment in 25 years. Quantitative estimates based on aerial photographs recorded an overall increase in woody plant cover of 27% between 1940 and 1985 (Le Roux 1996) and up to 59% between 1955 and 1998 (Hoffmann *et al.* 1999) in KwaZulu Natal.

Bush encroachment is considered undesirable by range and wildlife managers, mainly since it decreases grazing carrying capacity and is not aesthetically desirable in wildlife-reserves. Coupled with this are negative economic implications. Although bush encroachment has long been a widely recognized phenomenon in South Africa, the mechanism (the rate, pattern and dynamics) of the conversion from grass to woodland remains somewhat controversial.

There are several hypotheses on the causes of bush encroachment which have been reviewed in detail by Hoffmann *et al.* (1999). Bush encroachment is generally attributed to human activities and some of the causal explanations include overgrazing by livestock and related disturbance (Pratt and Gwynne 1977; van Vegten 1983; Noy-Meir 1982; Madany and West 1983; Skarpe 1990), reduced browsing pressure (Norton-Griffiths 1979; Prins and van der Jeugd 1993), change in fire regime (Norton-Griffiths 1979; Trollope *et al.* 1989) and change in climate (Hastings and Turner 1965; Neilson 1986; Trollope *et al.* 1989; Archer *et al.* 1995). Veld burning has, at times, been prohibited in SA for various reasons such as erosion control (e.g. in Kanthack 1907) and the tsetse fly control

period. Fire bans no doubt contributed greatly to bush encroachment since they created a window of opportunity for tree seedlings to become established, after which fire is no longer a tool for eradication (Scott 1970). In the Hluhluwe-Umfolozi Park (study area for this thesis) fire was banned during the anti-tsetse fly period (1947-1964) to prevent the wooden tsetse fly traps from burning. This is considered to be a major factor contributing to the escape of dense tree cohorts in the reserve. However there are other explanations for the dramatic densification of the tree layer which include the idea that seeds were released from predation due to the spraying of DDT during the anti-tsetse fly period which would have killed the bruchid beetles, the major predators of *Acacia* seed.

The decrease in grass production associated with bush encroachment (e.g. Trollope (1987) found a decrease of 46% in grass production over 6 years of severe *Acacia karroo* encroachment), reduces the stocking rates and habitat of indigenous animals, in addition to a more recent concern, visibility of wildlife.

Bush encroachment is a broad term used to describe a very diverse problem. If bush encroachment were restricted to one species in one place it may be easier to devise a method for its control. However bush encroachment, is caused by an array of species, and occurs in a range of habitats. In southern Africa, the most important of these are the deciduous species such as several acacias and *Dichrostachys cinerea* (Hoffmann *et al.* 1999). Some broad-leaved species are also categorised bush encroaching species.

What works in controlling bush encroachment in one set of circumstances may be ineffective in another with different environmental factors and species composition. It is likely that site factors, soil, climate (mainly rainfall) and species attributes are major determinants of tree response to range management techniques. However approaches to dealing with bush encroachment to date have largely ignored differences in species response to fire and have not been based on an understanding of the mechanism of tree response following disturbance. Perhaps as a result current methods in bush management are not effective.

1.5 Aim of this study

A major gap in savanna ecology is the lack of information on the biology of tree species and how they respond to disturbance. Given that fire is ubiquitous in savannas, and that it is also the most convenient management tool (Trollope 1980), it makes sense to investigate in more detail how it affects the tree layer. There has been a research focus on seeds and seedlings which some authors (Hoffmann 1996) consider to be of less importance in savanna dynamics than established trees. Thus, there is a need to improve our understanding of tree survival and regrowth following fire at the level of the individual. This study takes a detailed look at the biology of four savanna tree species, their life histories, survival and regrowth strategies in mesic savannas of South Africa. Tree response to varying types of injury is explored within and between species, in mesic and more arid environments. This study attempts to isolate the effects of fire on tree response by looking at different tree species and fire types. The study considers the response of established trees only and not seedling establishment and role of the seed bank. The degree to which the results from this research are limited to the study site are also discussed. It is hoped that this information will contribute to overall theory on tree – grass dynamics, influence thinking on veld management and provide direction for future research.

Management implications that are relevant for conservation as well as stock and game farming include:

1. controlling tree densities and maintaining open grassland
2. shaping tree architecture for browsing mammals (e.g. black rhino or goats)
3. shaping community structure and composition (i.e. ratio adults : juveniles or “gullivers”)

1.6 Thesis structure

This chapter has provided a general introduction on the sprouting behaviour of savanna trees, how this potentially influences recruitment with adult size classes in the face of disturbance by fire, and current management. This provides a context for the following chapters which take a detailed look at life history variation in growth and sprouting responses of four South African savanna tree species.

Chapter 2 explores the **biology of resprouting** in *Acacia karroo*, *A.nilotica*, *A.caffra* and *Dichrostachys cinerea* by means of clipping experiments. A basic model of tree response to injury is developed for these four species across tree height.

Building on Chapter 2, Chapter 3 explores tree response in *A.karroo*, *A.nilotica* and *D.cinerea* following **controlled burns** of different intensity and season. The role of bark thickness in explaining variation in tree response is investigated. I test the models of tree response developed by Higgins *et al.* (2000) in their individual-based, spatially explicit simulation model of grass and tree dynamics.

Chapter 4 investigates variation in response of trees to different **seasons of defoliation** by clipping. Plant phenology and root starch reserves are investigated as possible explanations for differences in response to season of clip.

Chapter 5 considers the **evolutionary ecology** of savanna trees. The savanna environment appears to have posed a strong evolutionary barrier to colonisation by trees of forest origins. What adaptations/exaptations are required for a tree to penetrate and survive successfully in savannas? Fires in mesic savannas occur at intervals as short as one to three years (Sarmiento 1983; Trollope 1993; Bond 1997). Such frequent fires pose a major hazard for tree recruitment. Tree seedlings not only compete with grasses directly, but also have to survive repeated burning yet grow tall enough to eventually emerge from the grass layer. In Chapter 5 I propose that recruitment of trees, especially in mesic savannas, is limited less by the availability of seeds or seedlings than by opportunities for escaping from the zone in which fires are sufficiently intense to kill aboveground stems. Many savanna trees have a distinctive set of adaptations that promote rapid height growth of juveniles out of zone of greatest fire damage. This results in a marked discontinuity between growth and reproductive patterns above and below the fire zone. Within the four study species I investigate whether they share any similar and distinctive life history features that allow recruitment despite frequent fires.

Chapter 6 is the concluding chapter of this thesis. Key findings are discussed in terms of their contribution to current knowledge of savanna dynamics as well as implications for veld management. Recommendations for future research are proposed.

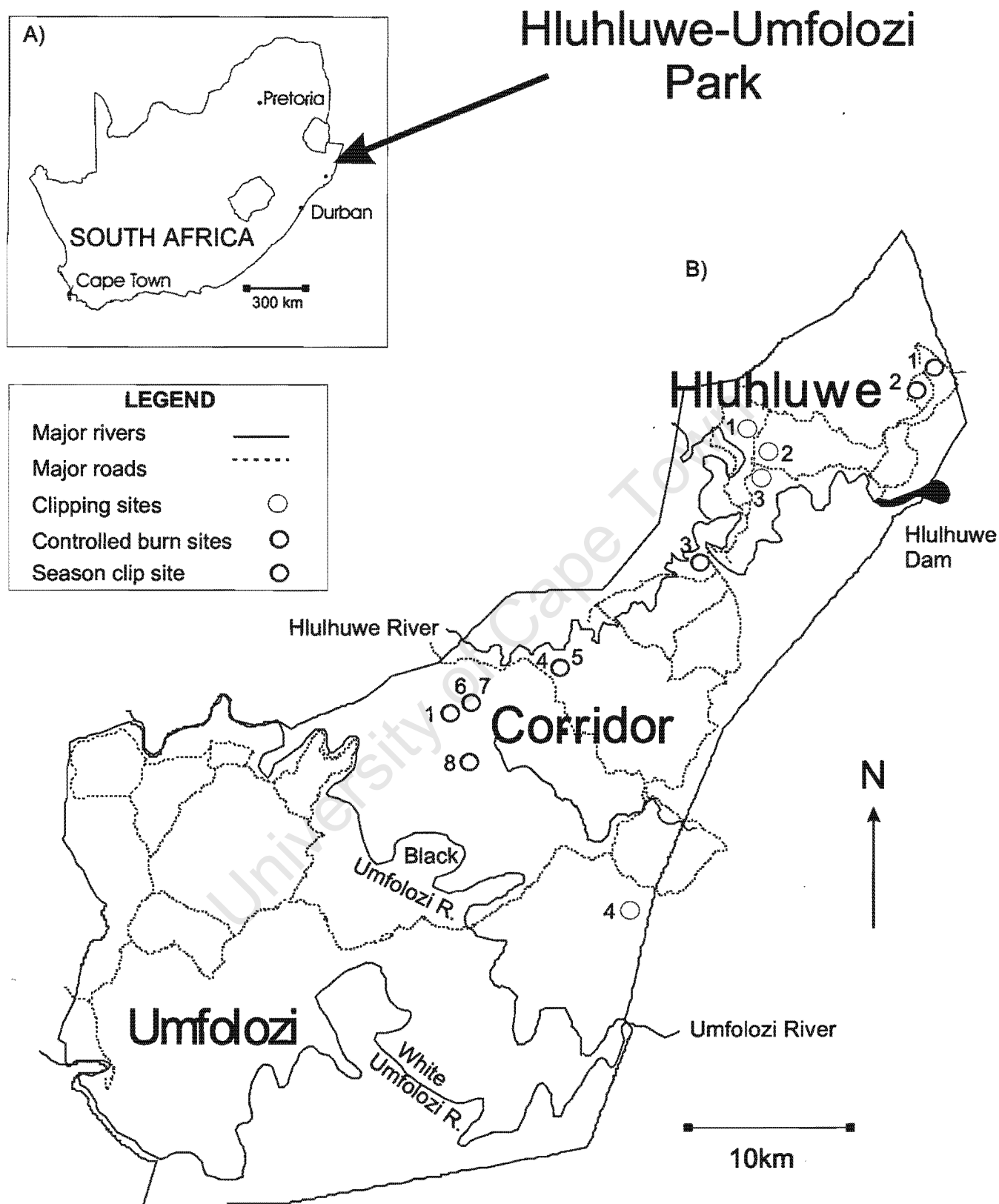


Figure 1.2 Map of the study area showing A) the location of the Hluhluwe-Umfolozi Park in South Africa, and B) the location of each of the study sites in the Hluhluwe-Umfolozi Park. The site numbers correspond to site names and details in Appendix A.

1.7 Study area and species

The study was conducted in Hluhluwe-Umfolozi Park (HUP), situated in northern Natal, South Africa (28° 00'S and 28° 26'S / 31° 43'E and 32° 09'E) (Figure 1.2 and Photos 1-2). The total area is approximately 1000km². The topography varies from hilly country and altitudes of approximately 750m in the north, to relatively flat country at a low of 60m in the south. Mean annual rainfall varies along the same altitudinal gradient from approx. 985mm in the north to 650mm in the south. The rainfall pattern is bimodal, with most rain falling in October and March, and June-August being the dry months (Brookes and MacDonald 1983). A layer of shales and sandstones underlie the HUP with frequent dolerite intrusions. Basic soil types are fine textured sandy clays. Study sites with comparable physical characteristics and species composition were chosen (Figure 1.2). The location, mean annual rainfall and soil types of each site are detailed in Appendix A.

The vegetation in this area falls within the lowland subcategory of Tropical Bush/Savanna and Zululand Thornveld (Acocks 1953) classified by Low and Rebelo (1996) as Natal Lowland and Central Bushveld. Most of the complex is dominated by woodland, savanna and thicket communities in which acacia species are abundant. *Themeda triandra* dominates the grass layer. The vegetation has been mapped and described in detail by Whately and Porter (1983). A steady progression from open grassland to woody thicket has been well documented over the last 60 years (e.g. Bourquin and Hitchins 1979; Foster 1955; Porter 1977).

Acacia karroo, *A. nilotica*, *A. caffra* and *Dichrostachys cinerea*, which occur frequently in the reserve, were chosen as the main study species throughout this study. Dense thickets of *A. karroo* and *D. cinerea* are particularly abundant throughout the reserve and especially in the more mesic parts. For detailed information on the study species, brief taxonomic descriptions and characteristics specific to the growth forms and subspecies occurring in HUP are contained in Appendix B.

Dense woody thickets characterise parts of the HUP and *A. karroo*, *A. nilotica* and *D. cinerea* are considered the most problematic thicket forming species in the mesic parts of the park. In some species there is an imbalance between the number of juveniles and adults found in

the reserve. There are very few mature *A.karoo* trees in the reserve especially the north and western corridor area of the HUP but gulliver stage plants are abundant and widespread. In contrast, mature *A.nilotica* trees are abundant and widespread forming woodlands over much of the reserve but juveniles are uncommon (Bond, Smythe, Balfour in press).

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1.8 References

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Photo 1 A relatively open ("unencroached") area in the corridor region of the Hluhluwe-Umfolozi Park in the dry season (August 1997).

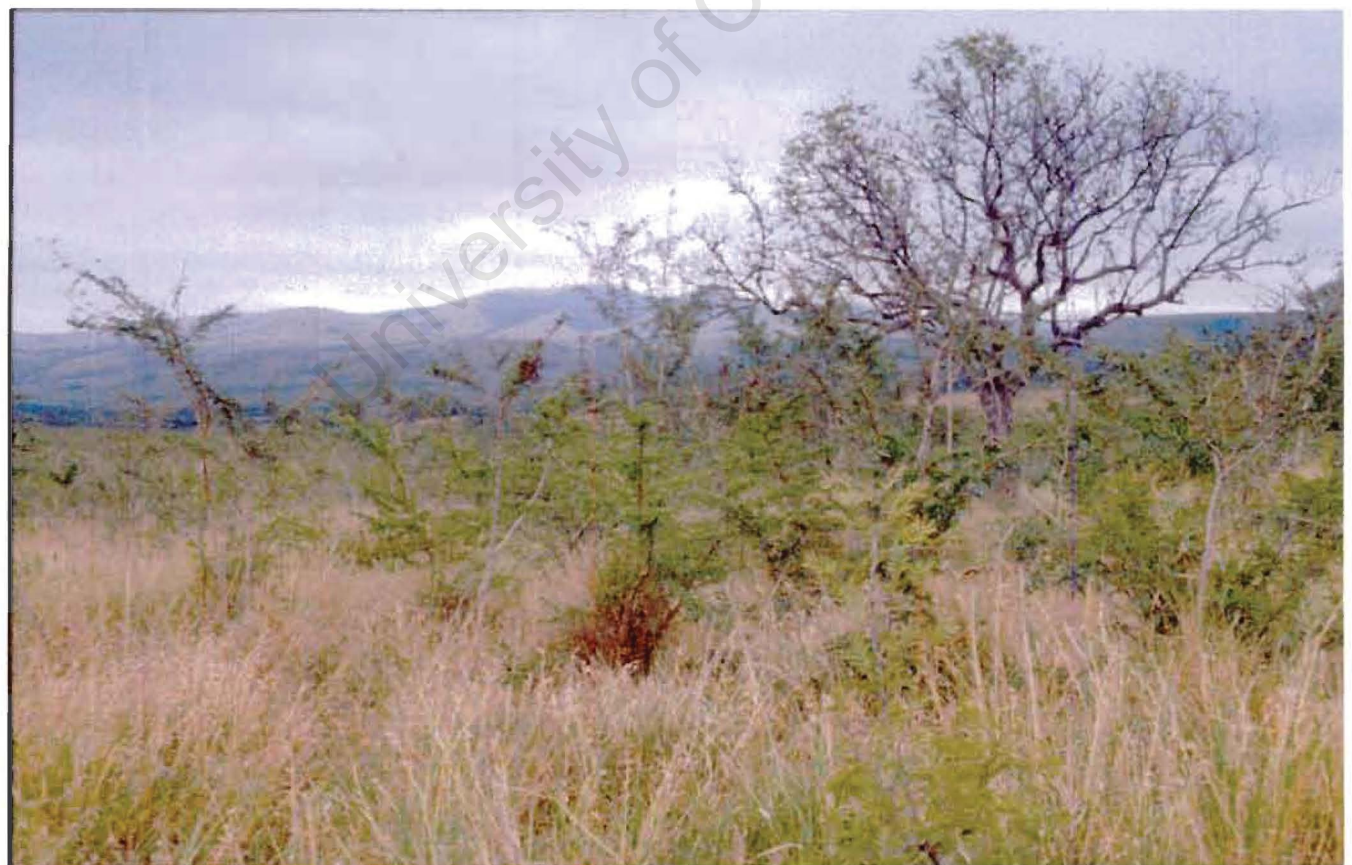


Photo 2 The typical vegetation structure of most of the study sites in the Hluhluwe-Umfolozi Park (August 1997). 1.5m-2.5m *Acacia karroo* gullivers dominate the scene. A few *Dichrostachys cinerea* plants with yellowish foliage are also pictured (front right).



Photo 3 Epicormic sprouting in *Acacia karroo* following a burn.



Photo 4 *Acacia caffra* reprotting from the rootstock following clipping.



Photo 5 *Acacia nilotica* resprouting following clipping at ground level. Note the thickness of the bark which is greater than that of *A. karroo* and *D. cinerea*.



Photo 6 Heavily browsed *Acacia karroo* gulliver.



Photo 7 *Acacia nilotica* gulliver two years post fire (topkilled).



Photo 8 *A.karroo* resprouting at two months after clipping.

2 THE RESPROUTING BIOLOGY OF FOUR WIDESPREAD TREE SPECIES IN THE HLUHLUWE-UMFOLOZI PARK

2.1 Introduction

In this chapter the ability of trees to resprout and the vigour of resprouting was investigated with the ontogeny of each species' life history by means of clipping experiments.

Resprouting ability depends on the availability of a bud bank. The variation in location of buds between and within species was investigated. I address the questions of when tree seedlings first acquire the ability to resprout and how long this sprouting ability maintained as a tree matures. The vigour with which trees resprout also varies and is most likely dependent on the stored carbon reserves. The rapid regrowth rate of trees in the first year following injury is likely to depend on these stored reserves, after which growth is based on current carbon uptake. This was tested by comparing rates of regrowth vigour at both high and low rainfall sites. Patterns of stem self-thinning across height classes and species may also elucidate further some of the different life history strategies of acacias. In later chapters (3-5) aspects of the ecology of resprouting are investigated, and results from clipping compared with those from controlled burns. A short introduction on resprouting biology is provided below.

2.2 Response of savanna trees to fire

Fire intensity, frequency and season play an important role in shaping and maintaining savanna vegetation communities in Africa. However, other than the ability to radically alter the savanna components (trees and grass), comparatively little is known about the mechanistic effects of fire regimes on the structural and functional dynamics of the ecosystem. The biological basis of the observed response of the tree component has received little research attention. Some studies have explored the effects of fire in savannas at the level of the individual tree (Hodgkinson 1998; Gignoux *et al.* 1997), but most studies have concentrated on ecosystem level processes. Currently there is no general predictive model on how different trees species will respond to injury following burning. Consequently

the use of fire for controlling tree densities in savannas is still haphazard and often ineffective.

Injury by fire and herbivory affect savanna trees by either: a) killing them outright; b) killing the aboveground parts only (referred to as "topkill") after which regrowth occurs from the stem base or root crown (Photo 4); or, c) scorching the aboveground parts and resprouting occurs from the stem or canopy (referred to as "epicormic sprouting") (Photo 3). The ability, mechanism and pattern of sprouting can vary greatly within and between genera and species. Resprouting is probably an early adaptive trait to injury (Wells 1969). The physiology of resprouting requires that a plant allocates resources to reserves in woody parts such as the roots, root crowns, stem bases, meristematic tissues and protective bark in some cases. Following injury, these reserves are mobilised to produce new growth and this could mean that there are fewer resources available for seed production and growth (i.e. as predicted by classic seeder-sprouter theory Keeley and Zedler 1978).

The seeder-sprouter trade-off has been well documented for woody plants in Mediterranean shrublands (Keeley and Zedler 1978; Cowling and Lamont 1987; reviewed in Bond and Midgley 2001). Non-sprouting species are characteristically killed by fire and rely solely on seed production for post-fire recruitment, allocating substantial energy to sexual reproduction. Conversely, resprouting species survive fire by resprouting, and they allocate less energy to sexual reproduction. Pate *et al.* (1990) found this trade-off pattern in south west Australia in congeneric species as did Keeley (1977) in *Arctostaphylos* in Californian chaparral.

This allocation trade-off has not been investigated in woody shrubs of savannas, perhaps because the classic seeder-sprouter life history trade-off pattern is not readily apparent in savanna trees, when compared with Mediterranean shrubs, such as in fynbos, where the ratio of seeders:sprouters in a community is strongly influenced by fire frequency. If seeder-sprouter life-history trade-offs do exist among savanna tree species, it is unknown how well they would account for the observed community structure. Given the dominance of resprouters in savanna systems, as well as their economic significance, it is surprising that the biology and ecology of sprouters at the level of the individual has received comparatively little attention.

In savannas, congeneric tree species show variation in their ability and pattern of resprouting following injury, but this pattern of variation and the underlying biological basis is not well understood. Several factors are thought to affect recovery including the size of the tree, and the intensity, season and frequency of injury. Variation in fire intensity influences tree mortality and tree architecture with the response often being size (height) dependent (Trollope 1984; Hodgkinson 1998). However, these patterns have seldom been quantified for savanna trees and shrubs, and the basis for inter and intraspecific variation is poorly understood (Flinn *et al.* 1992).

Explanations for this variation include factors such as the location of buds, bark form (e.g. degree of fissuring) and thickness, and tree architecture (Flinn *et al.* 1992). In the few studies that have addressed variation in sprouting ability, the explanations for variation remain mostly untested hypotheses. Hodgkinson (1986) found a high degree of variation within and between species in the resprouting ability in Australian Acacias. Gill (1995) suggested that a change in the distribution of shoot meristems may play a significant role in determining tree response to injury. Hobbs and Mooney (1985) documented a decrease in survival with increasing tree age following fire in the chaparral shrub, *Baccharis pilularis* spp. *consanguinea*.

The abovementioned studies can be distinguished by the explanations used for the variation in resprouting ability. They are either based on the location and size of the bud banks or on tree height.

Recently attempts have been made to link physiological and height related variation in tree response following injury. Bond and van Wilgen (1996) proposed the "Gulliver" strategy as a distinct life history in which, typically, multi-stemmed shrubs spend most of their life trying to escape the grass layer. When an opportunity arises (i.e. break in the fire or herbivory regime) a single stem escapes the "injury zone" (i.e. flame zone) to become an adult. However, this hypothesis has not yet been adequately tested. Dublin *et al.* (1990) described a similar strategy termed the *regeneration phase* in *Acacia tortilis* but did not elaborate on the full significance of these results. More recently Gignoux *et al.* (1997) recognised two distinct life histories in two resprouting savanna species (*Crossopteryx* and *Piliostigma*) and describe alternate fire survival strategies. These two strategies are: *Hide and resprout* (good root crown resprouting ability) and *stay and resist* (requires thick bark to withstand fire).

The importance of seeds and seedlings in savanna tree life histories is another poorly understood area of savanna ecology (reviewed in Midgley and Bond 2001). In arid savannas, seedling recruitment has been shown in some species and areas to be episodic (e.g. *Acacia mellifera* recruits in large cohorts during heavy rain events (Lloyd unpublished data)). Some researchers argue that seed and seedling ecology is less important in savanna dynamics than tree persistence once seedlings are established (Desmet *et al.* 1996; Higgins *et al.* 2000; Midgley and Bond 2001). Seedling recruitment therefore may not limit the number of adults in a population, but rather, the adult population size is limited by the number of opportunities, or windows for escape, for gullivers or juvenile trees from the grass layer. However case studies on the level and patterns of seedling recruitment have seldom been documented.

2.3 Aim of this study

This study makes use of clipping to investigate the variation in, and biological basis for, resprouting ability and regrowth vigour in four widespread savanna tree species across height classes, and a rainfall gradient. Clipping trees at different levels on the stem enables us to investigate the biology of resprouting. The study focuses on sprouting ability and regrowth vigour through the tree life history. I used *Acacia karroo* (Photo 6), *A. caffra*, *A. nilotica* (Photo 7) and *Dichrostachys cinerea*, as a model system to investigate variability in response of trees to injury, and the underlying causes. The comparative approach was used to develop a generalised model of tree response to burning using tree species that mature above and within the flame-zone. The Gulliver life history hypothesis of Bond and Van Wilgen (1996) was tested.

2.4 Methods

2.4.1 Study Area

The study was conducted in Hluhluwe-Umfoluzi Park (HUP), situated in KwaZulu Natal, South Africa (Chapter 1, Figure 1.2). See Chapter 1 and appendix A for a detailed description of the study area and each site. Study sites with comparable physical

characteristics and burning histories were chosen for the clipping experiments. The location, mean annual rainfall and soil types of each site are detailed in Appendix A.

2.4.2 Experimental Approach

Clipping experiments were used as an analogue for fire and herbivore injury. Clipping has the advantage, over wild fires and other forms of injury, of greater control on the location and type of injury. Clipping experiments were designed to investigate variation in **resprouting ability** as well as the **resprouting vigour**.

Firstly, to investigate variation in **resprouting ability** (i.e. availability of a bud bank) I looked at the following:

- 1) where the buds or meristematic tissues are situated
- 2) the number of buds at each location
- 3) height dependent tree survival
- 4) age when seedlings first acquire sprouting ability
- 5) the resprouting ability of adult trees

Secondly, to investigate variation in **resprouting vigour** (i.e. based on stored reserves) I looked at the following:

- 1) the rate of tree height regrowth
- 2) the rate of decline/self thinning of resprouting stems with time
- 3) the sum of the length of all resprouting stems as an indication of the stored root reserves
- 4) the variation in resprouting response in an arid versus mesic site

2.4.3 Clipping treatments

In July 1995 three clipping (stem removal) treatments representing different levels of injury were applied to individuals of four tree species across four height classes (Figure 2.1). The three clipping treatments were: **A** - all stems removed to ground level (equivalent to topkill – defined in this study as death of all above ground parts); **B** - all stems and rootcrown tissue removed to 5cm belowground; and **C** - all stems removed to 10cm above ground. These three clipping treatments provide a useful means for locating meristematic buds. Treatment

B represents severe injury to the root crown, and is not likely to occur naturally, but rather served to locate bud banks.

Clipping treatments were replicated on approximately ten individuals of each species in each height class. Although these four species are widespread throughout most of HUP, some height classes were absent from the chosen study sites (and indeed were rare throughout the rest of the HUP). Replication was therefore reduced or absent in these cases. (e.g. in *A.caffra* in the <0.5m height class and in *A.nilotica* in the 1.5-2.5m height class no trees were found in the study area). The >2.5m height class comprised fairly large trees (i.e. ones that have escaped the flame zone) and these received clipping treatment C only, due to the labour requirements of executing the other two clipping treatments, particularly clipping treatment B. Further, clipping treatment C would be the closest approximation to the most detrimental naturally induced injury in large trees. Clipping treatments were allocated randomly to trees in each height class.

For a comparison of tree response and growth rates at lower rainfall, trees of three of the same species in the 0.5-1.5m height class were clipped at ground level (clipping treatment A) at a more arid site in HUP (approx. 650mm/yr) (see Chapter 1, Figure 1.2).

2.4.4 Pre-clip and regrowth measurements recorded

Prior to clipping, tree height and number of stems was recorded for all individuals. Clipped trees were marked with numbered metal tags on wire stakes that were placed in the ground at the base of the tree. Each tree's position was mapped for future location. Bark thickness of the cut stems was measured and the data used in Chapter 3.

In September 1995 (2 months after clipping), July 1996 (12 months after clipping) and July 1997 (24 months after clipping) all clipped trees were relocated and regrowth measurements recorded. Three measures of regrowth vigour are used: sprout height, number of resprouting stems (resprouting stems were divided into primary and secondary resprouting stems according to their size) and the sum of the length of all resprouting stems (measured as length of stems sprouting from ground level, branches on stems not added to length). I recorded whether each tree was dead or alive, the origin of resprouting stems (i.e. root crown or stem); and incidence of browsing on regrowth.

CLIPPING TREATMENTS

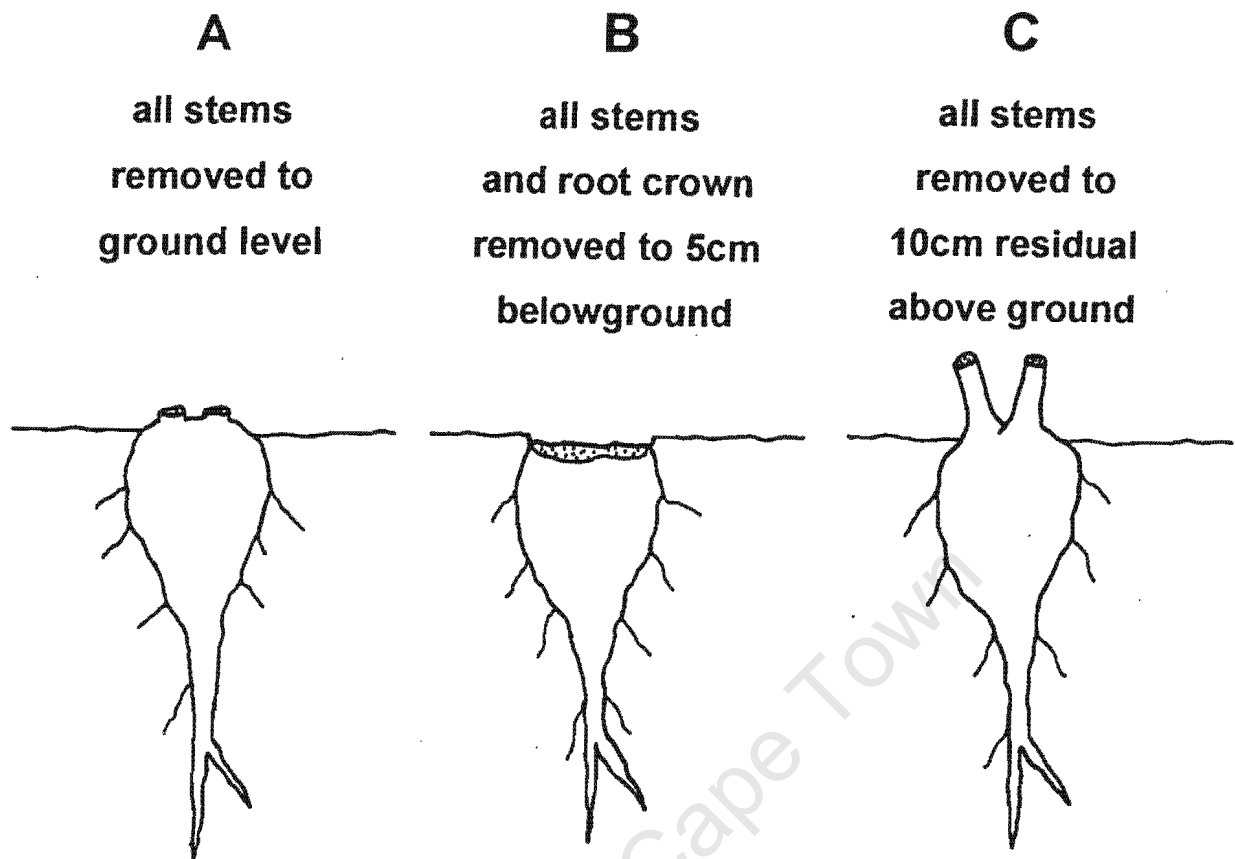


Figure 2.1 Diagrammatic representation of the three clipping treatments applied to four tree species across various heights. These clipping treatments were used as analogues for fire or herbivore injury.

2.4.5 Seedling response to clipping

Seedlings of all species were either not present or very difficult to locate in the field. To measure the resprouting ability of 6 month old tree seedlings, seeds were germinated and planted out in a field adjacent to the Hluhluwe Research Centre garden. The plot was cleared of other plant material when the seeds were planted after which grass and weeds were allowed to establish. After 6 months all seedlings were marked with numbered tags, and the following measurements were recorded: seedling height; number of resprouting stems; and the length of each stem. Half of the seedlings were clipped at ground level (i.e. treatment A) and the other half served as controls. Six months and 12 months later response of clipped seedlings and growth of the controls was measured.

2.5 Results

2.5.1 Variation in resprouting ability

2.5.1.1 General characteristics

The four study species had very different growth habits. In all species, resprouting trees had two different types of resprouting stems that I classified as either primary (one to two (or more) tall, thick and upright stems) or secondary stems (several short, thin stems usually having a more decumbent, sometimes etiolated growth habit) (Figure 2.2). The shorter secondary stems were classified as those with a basal diameter less than approximately one tenth of the thickest stem diameter. *A.nilotica* had fewer primary stems than *A. karroo* and *D.cinerea*, while *A.caffra* had many more dominant stems and fewer secondary stems. In all species secondary stems generally originated from the root crown.

The size of the root crown and root structure differs between species. *D.cinerea* has a system of narrow lateral (non-tap) roots compared with the acacias, which had larger tap root systems and large root crowns (Photo 13 and 14). A schematic representation of each species' architecture (growth habit/form) across height classes is illustrated in Figure 2.2. Adults of all species were single-stemmed except *A.caffra*.

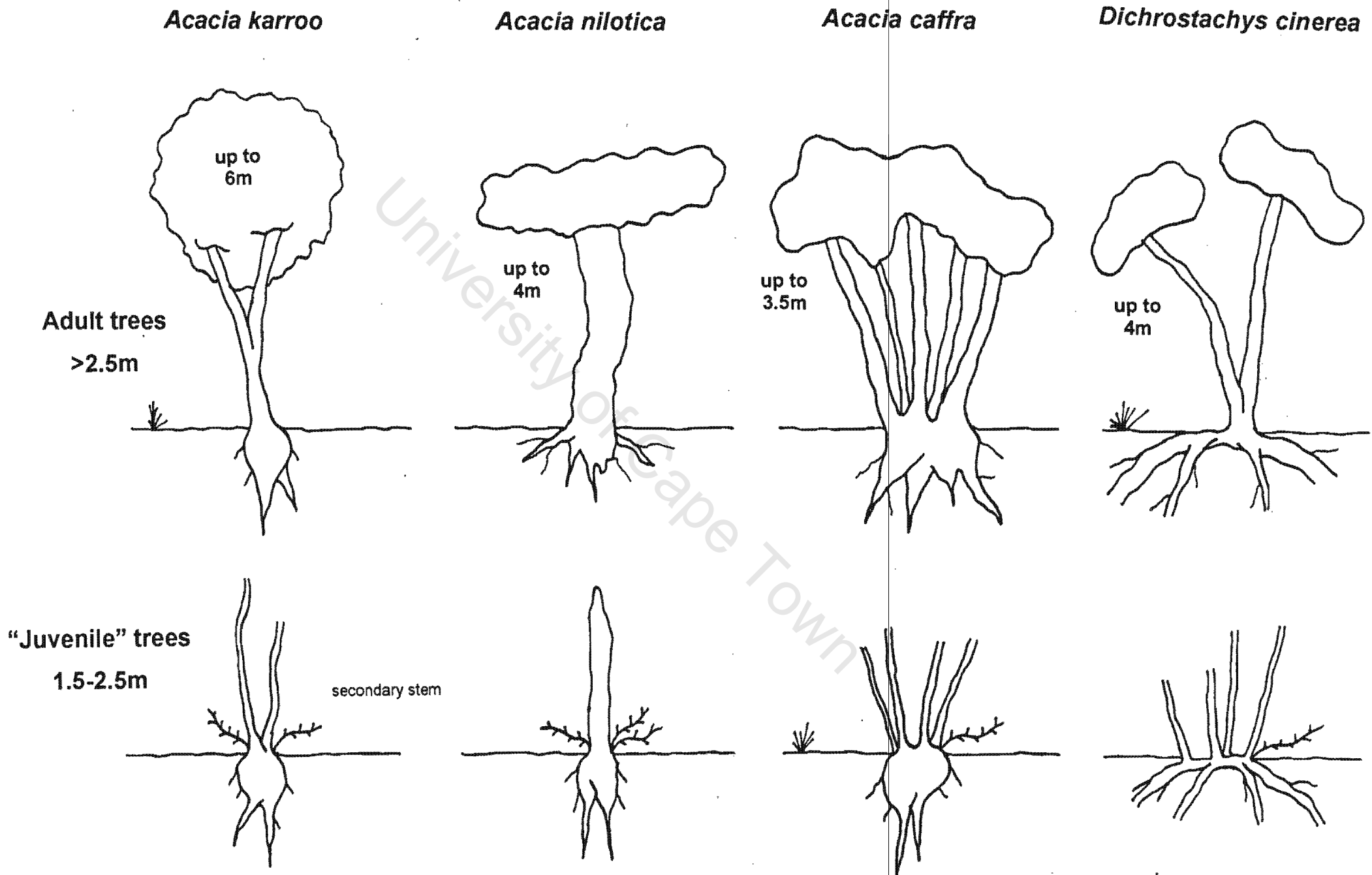


Figure 2.2 Sketches of typical tree architecture/growth form of juveniles and adults of the four study species.

2.5.1.2 Height dependent survival

2.5.1.2.1 Patterns of mortality across height classes

Figure 2.3 shows the proportion of tree mortality (including seedling mortality data) across the four species combined for all clipping treatments. Mortality was only evident in very young seedlings and mature trees, except in *A.nilotica* where mortality was also evident in trees <0.5m. Tree mortality varied less between species than within species, where mortality varied across height classes. All species, except *A.caffra* which showed less than 10% mortality, showed >70% mortality in the >2.5m height class. In 6-month-old seedlings in most species there was approximately 50% mortality.

2.5.1.2.2 Effects of different clipping treatments

The relative importance of each clipping treatment in terms of tree mortality was presented in Table 2.1. Treatment comparisons are based on qualitative, visual assessments of means and standard deviations. Only in *A.nilotica* was there an obvious clipping treatment effect on mortality, where treatment B caused higher mortality rate in height classes sampled.

2.5.1.3 Location and size of bud banks

The three clipping treatments were useful for locating the active buds banks in each species, while the number of resprouting stems gives an indication of the size of the bud banks.

2.5.1.3.1 Variation in origin of resprouting stems across species, clipping treatments and height classes

The origin of resprouting stems varied depending on the species, clipping treatment and height class. In most species resprouting occurred from the stem area immediately subtending the cut (clipped) line. Resprouting stems originated either from the root crown or stem (epicormic) between ground level and 10cm aboveground (Photo 4-5). Table 2.2

shows the proportion of primary stems arising from the root crown and the stem in surviving plants, for each species, height class and clipping treatment. In all four species secondary stems originated mainly from the root crown. Some species regenerated from both the root crown and stem, e.g. mainly *A.karoo*. In September 1995 (2 months after clipping) it was not possible to distinguish between primary and secondary stems since they were too small (Photo 8). This was also the case in the <0.5m height class, where few or no secondary stems were recorded.

Following clipping treatments A and B, all species resprouted from the root crown or stem at ground level. *A.nilotica* showed the poorest response following treatment B (Table 2.2).

Clipping treatment C caused the greatest variation in patterns of resprout origin between species and height classes. Following clipping treatment C and across all height classes of *A.nilotica* and *A.caffra*, resprouting stems originated mainly from the stem. This suggests that there are more buds on the stem than in the root crown. Following clipping treatment C, trees smaller than 1.5m in *A.karoo* resprouted mainly from the stems, and trees greater than 1.5m resprouted mainly from the root crown. A similar pattern was found for *D.cinerea* except that trees smaller than 1.5m produced equal proportions of resprouting stems from stem and root crown. Of all the study species, *D.cinerea* showed the poorest ability to regenerate from the stem following clipping treatments C. In *D.cinerea*, trees of 1.5-2.5m resprouted from the crown following clipping treatments A and C. This suggests a possible loss of epicormic resprouting ability with increasing height.

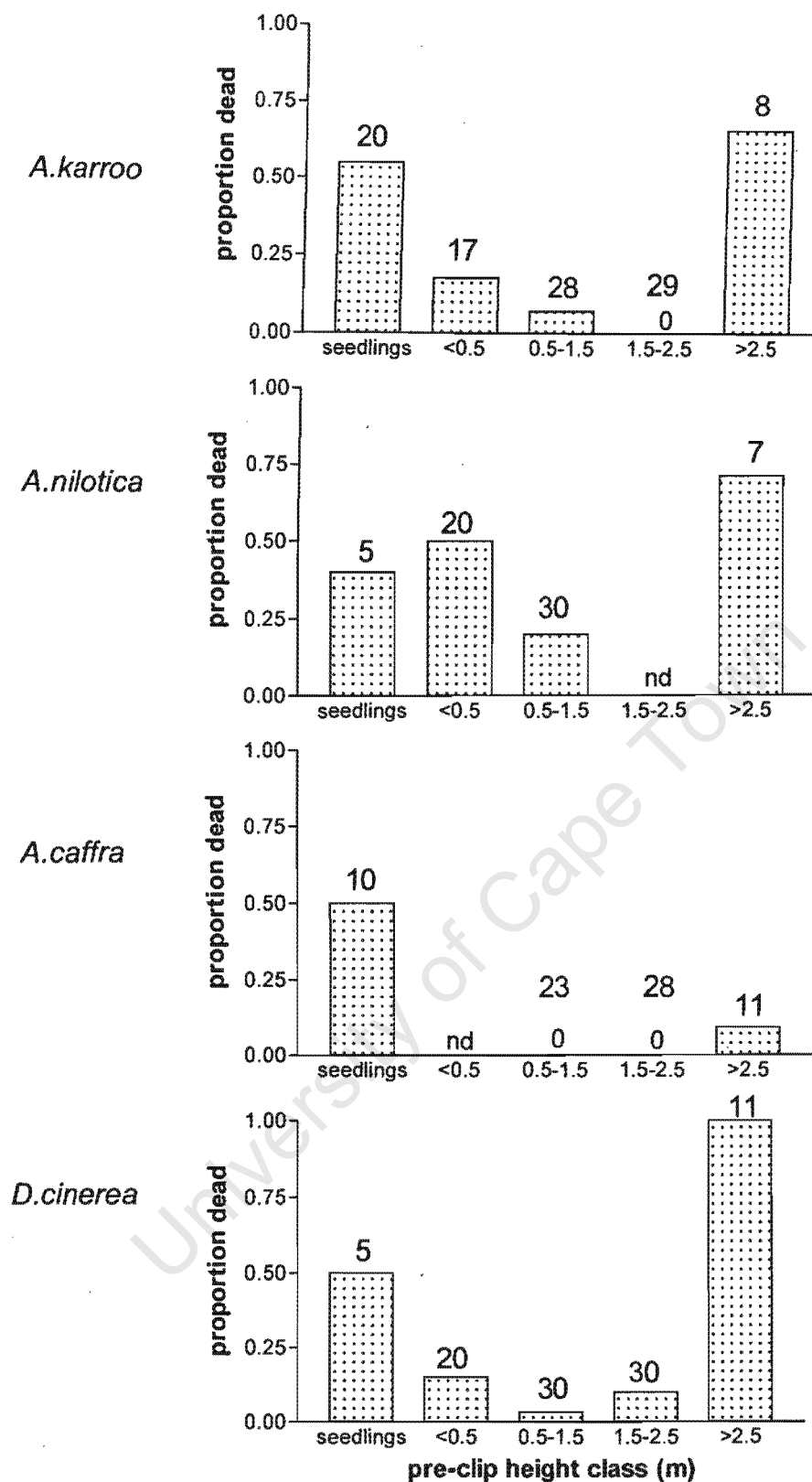


Figure 2.3 Proportion of trees that died following clipping, for each pre-clip height class. The proportions are combined for all clipping treatments. Tree mortality was recorded up to two years post clip but there was very little mortality in year two. Numbers above the bars represent the sample size.

Table 2.1 Proportion of trees that died following each of the 3 clipping treatments (A, B and C) across 5 height classes. (Sample size in parenthesis.) (Figure 2.3 shows the combined mortality for all treatments). (nd = no data collected).

SPECIES	Treatment	HEIGHT CLASS (m)				
		Seedlings	<0.5	0.5-1.5	1.5-2.5	>2.5
<i>A.karoo</i>	A	0.55 (20)	0.125 (8)	0 (8)	0 (8)	
	B		0.222 (9)	0.091 (11)	0 (10)	
	C		nd	0.111 (9)	0 (11)	0.667 (8)
	combined	0.55 (20)	0.176 (17)	0.071 (28)	0 (29)	0.667 (8)
<i>A.nilotica</i>	A	0.4 (5)	0 (10)	0.1 (10)	nd	
	B		1 (10)	0.5 (10)	nd	
	C			0 (10)	nd	0.714 (7)
	combined	0.4 (5)	0.5 (20)	0.2 (30)	nd	0.714 (7)
<i>A.caffra</i>	A	0.5 (10)	nd	0 (9)	0 (11)	
	B		nd	0 (6)	0 (4)	
	C			0 (8)	0 (13)	0.091 (11)
	combined	0.5 (10)	nd	0 (23)	0 (28)	0.091 (11)
<i>D.cinerea</i>	A	0.5 (5)	0.3 (10)	0 (10)	0.1 (10)	
	B		0 (10)	0.1 (10)	0.1 (10)	
	C			0 (10)	0.1 (10)	1 (11)
	combined	0.5 (5)	0.15 (20)	0.033 (30)	0.1 (10)	1 (11)

Table 2.2 Proportion of primary resprouting stems arising from the root crown and the stem area in surviving trees, following three different clipping treatments. (nd = no data collected)

SPECIES	HEIGHT CLASS (m)	CLIPPING TREATMENT					
		A ground level		B below ground		C above ground	
		CROWN	STEM	CROWN	STEM	CROWN	STEM
<i>A.karoo</i>	<0.5	1.0	0.0	1.0	0.0	nd	nd
	0.5-1.5	1.0	0.0	1.0	0.0	0.11	0.88
	1.5-2.5	0.9	0.1	1.0	0.0	0.91	0.09
	>2.5	nd	nd	nd	nd	0.875	0.125
<i>A.nilotica</i>	<0.5	0.91	0.09	0.0	0.0	nd	nd
	0.5-1.5	0.875	0.125	0.8	0.2	0.3	0.7
	1.5-2.5	nd	nd	nd	nd	nd	nd
	>2.5	nd	nd	nd	nd	0.0	1.0
<i>A.caffra</i>	<0.5	nd	nd	nd	nd	nd	nd
	0.5-1.5	0.9	0.1	1.0	0.0	0.25	0.75
	1.5-2.5	1.0	0.0	nd	nd	0.15	0.85
	>2.5	nd	nd	nd	nd	0.1	0.9
<i>D.cinerea</i>	<0.5	1.0	0.0	1.0	0.0	nd	nd
	0.5-1.5	1.0	0.0	1.0	0.0	0.6	0.4
	1.5-2.5	0.857	0.143	1.0	0.0	1.0	0.0
	>2.5	nd	nd	nd	nd	0.0	0.0

Table 2.3 Mean number (and standard deviation) of primary and secondary stems measured in 1 year (1996) and 2 years (1997) after clipping. Results are shown for clipping treatment A only as it is the closest surrogate for topkill. (nd = no data available).

SPECIES	TIME SINCE CLIP	HEIGHT CLASS										
		seedlings		<0.5			0.5-1.5			1.5-2.5		
		1°	n	1°	2°	n	1°	2°	n	1°	2°	n
<i>A.karoo</i>	1yr	1.67 (0.94)	15	1(0.5)	0.5 (1)	8	2.17 (1.46)	0.33 (0.62)	12	3.2 (1.72)	0.8 (1.08)	10
<i>A.karoo</i>	2yr	0.75(0.94)	9	1.13 (0.60)	0 (0)	8	1.25 (0.43)	0 (0)	12	2.3 (1.79)	0 (0)	10
<i>A.nilotica</i>	1yr	2.5 (0.5)	3	2.5 (1.5)	0.3 (0.64)	10	1.4 (0.92)	1.6 (2.24)	10	nd	nd	0
<i>A.nilotica</i>	2yr	2(1.41)	3	1.5 (0.92)	0 (0)	10	0.9 (0.7)	0 (0)	10	nd	nd	0
<i>A.caffra</i>	1yr	1.2(1.08)	10	nd	nd	0	2.78 (1.69)	0.78 (0.79)	9	3.09 (1.56)	5.36 (2.1)	11
<i>A.caffra</i>	2yr	1.3(1.55)	5	nd	nd	0	1.44 (0.68)	0 (0)	9	2.99 (1.16)	0 (0)	11
<i>D.cinerea</i>	1yr	1.25(0.5)	4	1.56 (1.42)	0 (0)	10	1.6 (1.11)	0.7 (0.9)	10	4.6 (2.97)	2 (2.28)	10
<i>D.cinerea</i>	2yr	1(0.82)	3	0.7 (0.9)	0 (0)	10	1.5 (0.5)	0 (0)	10	2.9 (1.76)	0.4 (0.92)	10

2.5.1.3.2 Variation in number of resprouting stems across species, clipping treatments and height classes

Figure 2.4 shows the mean number of resprouting stems produced in each species across height classes and three clipping treatments. The pre-clip number of stems and number of resprouting stems produced at 2, 12, and 24 months post-clip are shown. All seedlings were single stemmed before clipping. Table 2.3 shows the relative contribution of primary and secondary stems, and how numbers change over two years.

In *A.karoo* the number of resprouting stems was greater than the pre-clip number. Over time the decrease in resprout number was attributed to die-off in secondary stems (Table 2.3). In *A.karoo* there was very little variation in number of resprouting stems between clipping treatments, except in the 0.5-1.5m height class where clipping treatment B produced half the number of resprouting stems compared with clipping treatment A two months post clip. In year 1 and 2 the number of resprouting stems produced following treatment A decreased to match that of treatment B. In 1.5-2.5m *A. karoo* trees, clipping treatment C produced less than half the number of resprouting stems compared with

clipping treatment A and B. This may be due to fewer meristematic buds on the stem or apical dominance of the 10cm stem. The 1.5-2.5m pre-clip tree height produced the highest number of resprouting stems. In seedlings that were clipped, the number of stems increased in the first year and then decreased to single stemmedness in the second year after clipping.

In *A.nilotica* clipping treatments had a greater effect on variation in the number of resprouting stems produced, particularly for the 0.5-1.5m height class, which produced the greatest number of resprouting stems following clipping treatment C. Conversely, the 0.5-1.5m height class, produced the lowest number of resprouting stems following clipping treatment B, perhaps because there are few buds in the root crown. Relative to the pre-clip number of stems, trees in the >2.5m height class produced the lowest number of resprouting stems. In seedlings that were clipped, the number of stems increased in the first year and then decreased slightly, but remained multi-stemmed in the second year after clipping.

In *A.caffra* clipping treatment B produced equal or fewer stems than the pre-clip number. Clipping treatment C produced the highest number of resprouting stems relative to the pre-clip number of stems. The 1.5-2.5m height class was the most vigorous, producing almost twice the number of pre-clip number stems following treatments A and C. Clipped seedlings remained mostly single stemmed in the first and second year after clipping.

In *D.cinerea* clipping treatments A and B produced the same number of resprouting stems as the pre-clip number of stems. Clipping treatment C produced the highest number of resprouting stems in all height classes. Across height classes, there was no difference in number of resprouting stems except in the >2.5m class where 100% mortality was observed. Clipped seedlings remained mostly single stemmed in the first and second year after clipping.

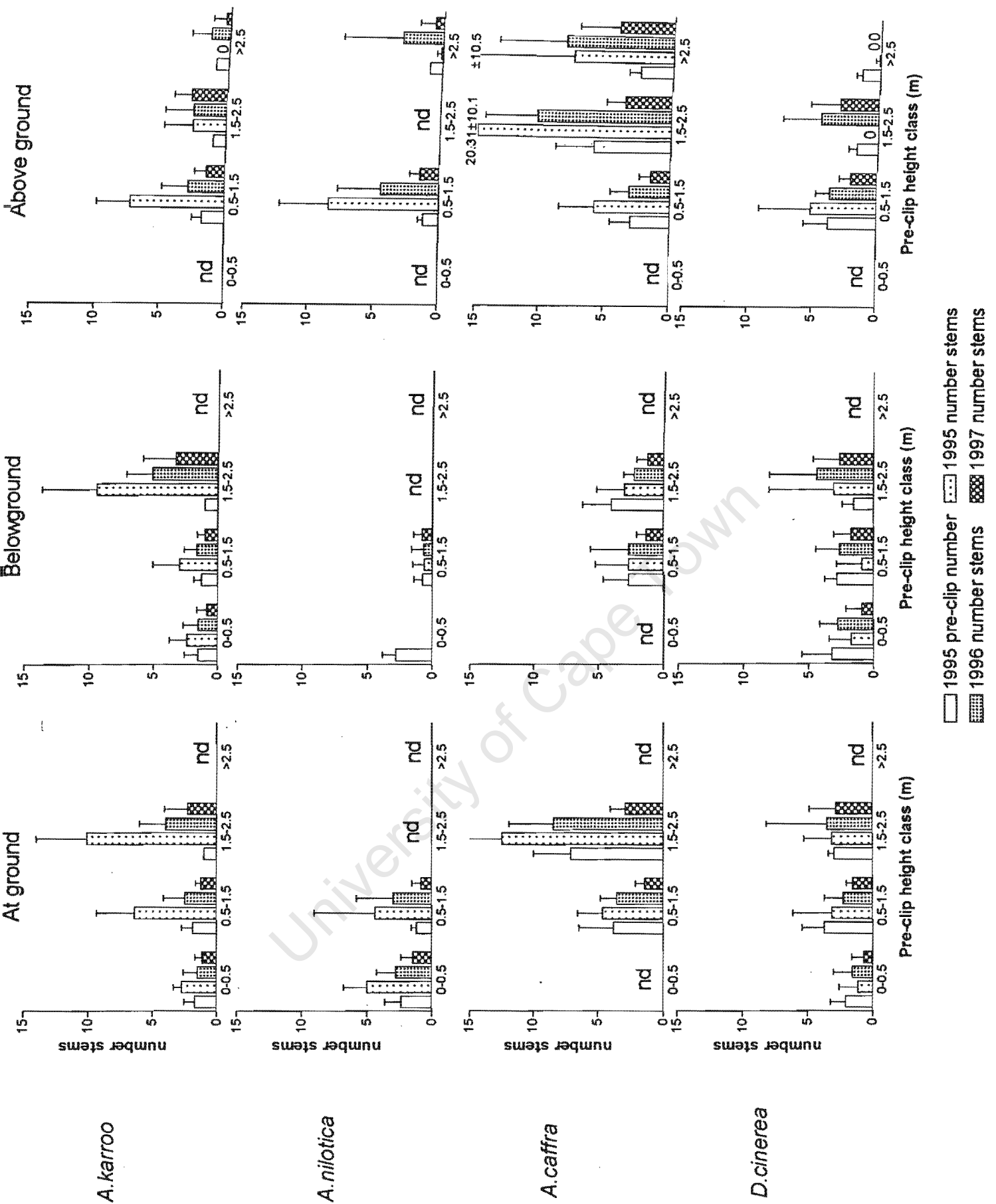


Figure 2.4 Mean number (and standard deviation) of resprouting stems produced per plant recorded in 1995 pre-clip measurement, and regrowth measurements recorded three months (1995), 1 year (1996) and 2 years (1997) after clipping. Illustrated here for the three clipping treatments, four species and four height classes. Averages for the regrowth measurements are the sum of primary and secondary stems. (nd = no data collected; 0 = all dead).

2.5.2 Variation in resprouting vigour

Resprouting vigour cannot easily be quantified by a single measurement, since for example, two trees of the same height may differ tenfold in the number of resprouting stems produced. Therefore in this study three different measurements of resprouting vigour were used to quantify variation in tree response to injury. Regrowth height is indicative of the rate at which a plant can reach escape height after a fire. The sum of the length of all resprouting stems gives an indication, particularly in the first year following injury, of stored energy reserves. In subsequent years, the sum of the length of all resprouting stems, gives an indication of growth rate based on current carbon uptake.

For each of these regrowth measurements, means and standard deviations are presented as bar graphs, exhibiting the differences between: species; height classes; clipping treatments; and time since clipping.

2.5.2.1 Height recovery

In Figure 2.5.1 of regrowth height versus pre-clip height, the straight line represents regrowth equal to the pre-clip height. The location of a point indicates how fast trees are able to attain, or exceed, their pre-clip height following injury. Figure 2.5.1 also shows that the height classes delimited in the study are appropriate in terms of capturing the patterns of tree response. Results from clipping treatment A and C are combined since there was no difference in response between clipping treatments. Figure 2.5.2 shows bar graphs of pre-clip and regrowth height at 2, 12 and 24 months post clip. Figure 2.5.3 shows height regrowth following clipping and in controls in seedlings of the study species. Of all height classes and in all species, seedlings show the lowest regrowth vigour.

In *A.karoo* height regrowth was highest for <0.5m and 0.5-1.5m height classes where 1 and 2 years regrowth heights respectively, were greater than the pre-clip height (Figure 2.5.1 and 2.5.2). Trees in the <0.5 height class had regrown up to 3 times taller after two years since clipping. Trees in the >2.5m height class show the lowest regrowth vigour. *A.karoo* seedlings only regained their pre-clip height after 2 years (Figure 2.5.3).

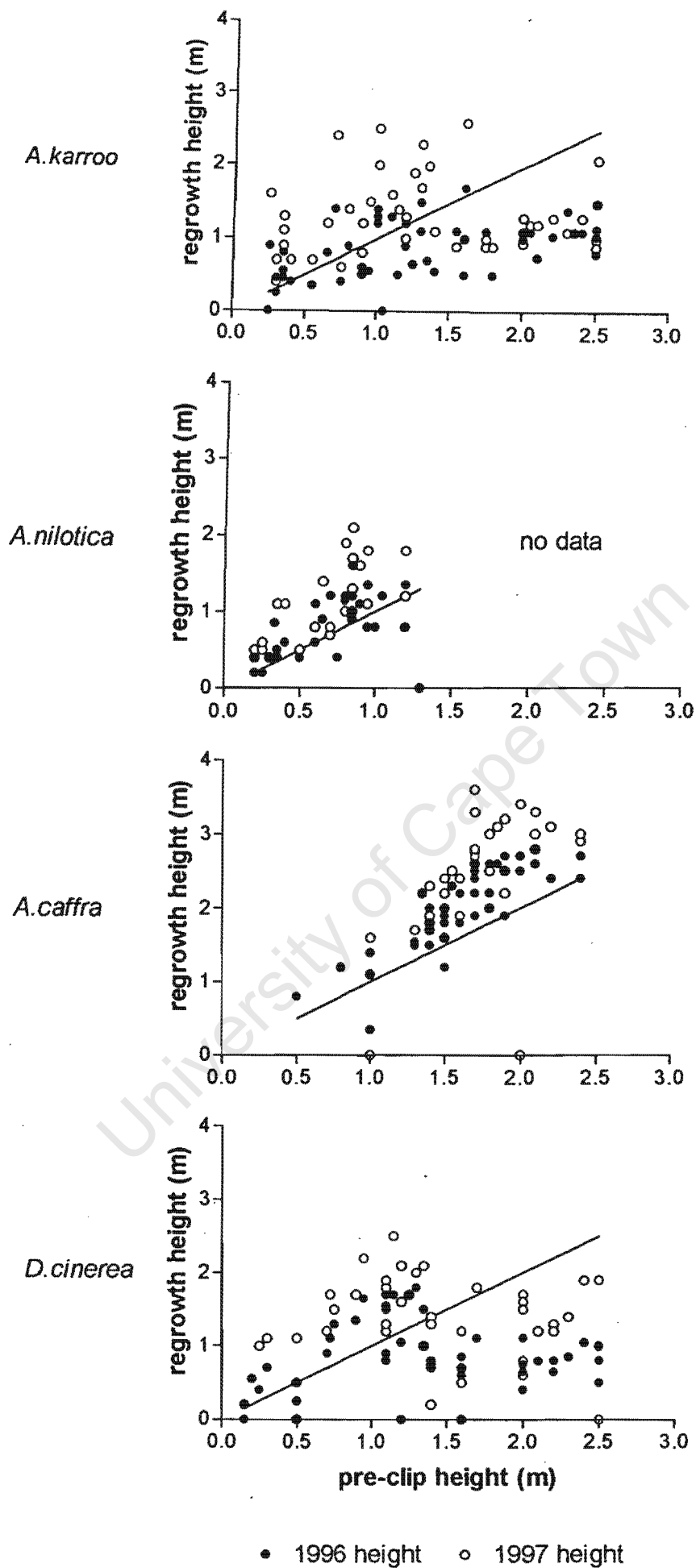


Figure 2.5.1 X-Y plots of pre-clip height and regrowth height measurements taken in 1996 and 1997 (i.e. one and two years post clipping). The diagonal indicates where pre-clip height = post-clip height.

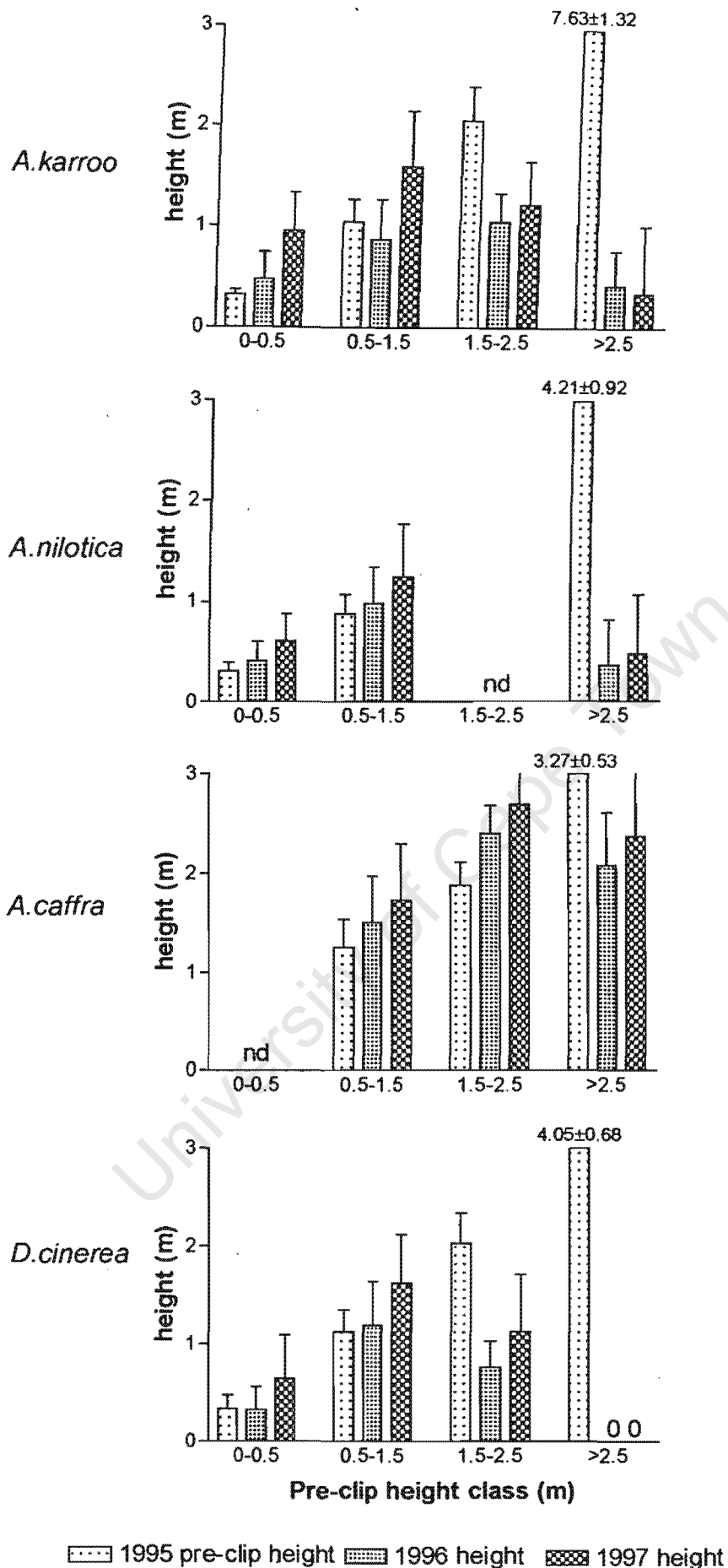


Figure 2.5.2 Mean heights (and standard deviations) recorded: 1995 pre-clip, 1996 regrowth, and 1997 regrowth. Illustrated here for the combined results of clipping treatment A and C, for each of the study species and four height classes. (nd = no data collected; 0 = all dead).

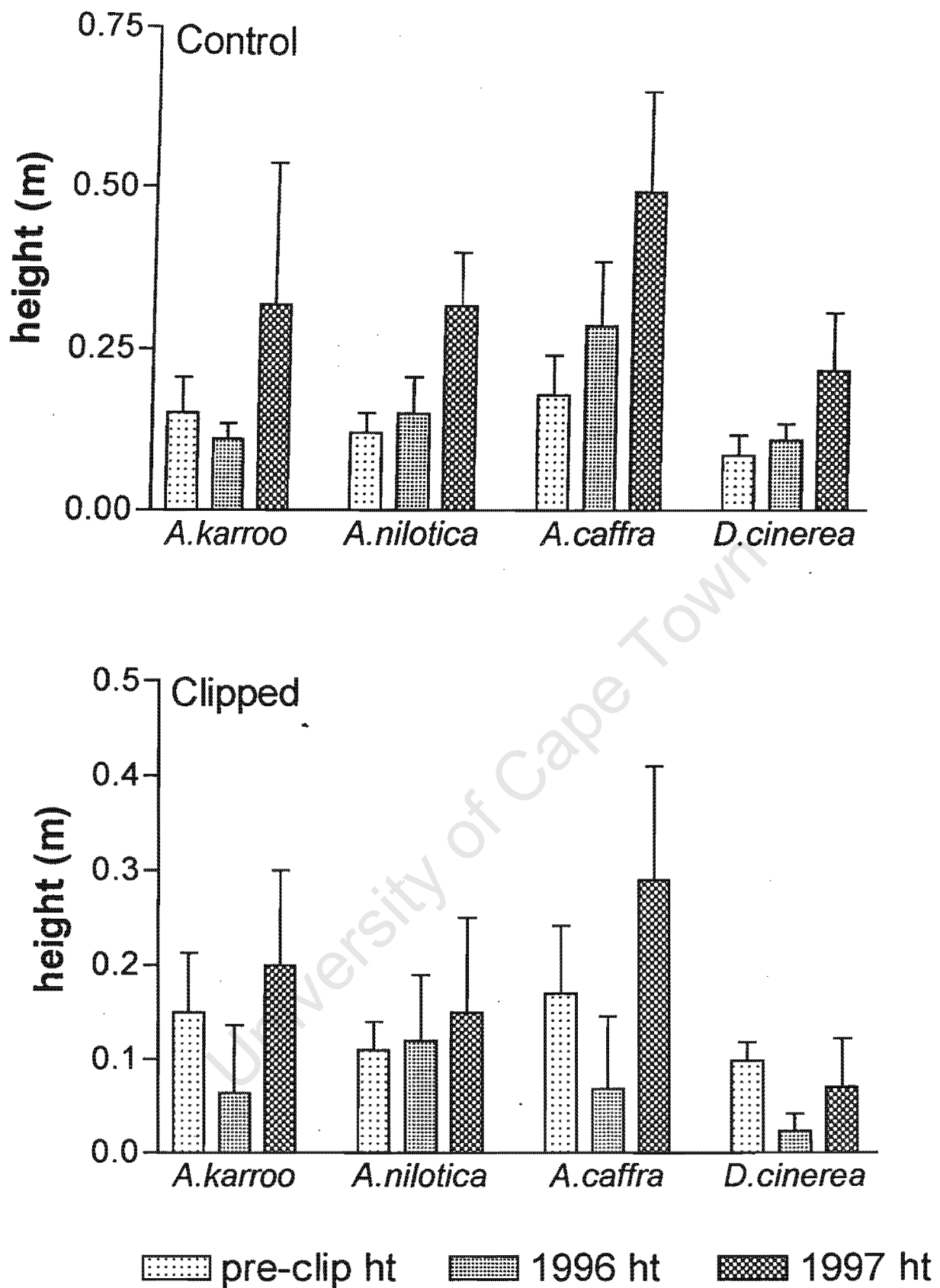


Figure 2.5.3 Mean height growth (and standard deviation) of seedlings of the study species after 6, 12 and 24 months. Half of the seedlings were clipped at 6 months and the other half serve as controls. These seedlings were planted out.

In *A.nilotica* plants in the 0.5-1.5m height class regained and exceeded the pre-clip height 2 years after clipping. Trees in the >2.5m height class height class showed drastically reduced height regrowth following clipping (Figure 2.5.1 and 2.5.2). *A.nilotica* seedlings regained pre-clip height after 1 year although the sample size was too small in this case to be significant (Figure 2.5.3).

In *A.caffra* height regrowth across height classes always exceeded pre-clip height in all height classes, except in the >2.5m height class where trees reverted to a lower height class. However *A.caffra* was not as negatively affected as the other species in the same height class (Figure 2.5.1 and 2.5.2). *A.caffra* seedlings regained and exceeded pre-clip height after 2 years (Figure 2.5.3).

In *D.cinerea* regrowth height was proportional to pre-clip height across all height classes, except the >2.5m height class where mortality was 100% (Figure 2.5.1 and 2.5.2). *D.cinerea* seedlings had not regained pre-clip height after 2 years (Figure 2.5.3).

2.5.2.2 Rates of stem self-thinning

Figure 2.4 shows the number of pre-clip stems and resprouting stems across species, clipping treatments and height classes. The decline in number of resprouting stems between the first and second year since clipping, is shown in Table 2.3, for clipping treatment A only. In *A.karoo*, the number of resprouting stems rapidly decreased to approximately half the original number after 1 year of regrowth across all three clipping treatments (Figure 2.4). In *D.cinerea* the number of resprouting stems increases slightly after the first record at 2 months post clip. This was because *D.cinerea* lagged behind the other study species in terms of phenology (i.e. *D.cinerea* only began leaf-flush at 2 months whereas other species had already begun leaf-flush). Table 2.4 (based on data in Table 2.3) shows the rate of decline in the number of resprouting stems (primary and secondary combined) over time as:

$$\text{Rate of decline in number stems} = t_1 (\text{no. stems}) - t_2 (\text{no. stems}) / t_1 (\text{no. stems})$$

Table 2.4 The fraction of stems surviving relative to the total number of stems produced as calculated for two different time-frames (*n* in brackets) for trees following clipping treatment A in three height classes. Rate was calculated as proportion of decrease in resprouting stems over each time period (see equation above). Two self thinning rates are shown for different periods (i.e. from 2 months post clip to 2 years, and from 1 year post clip to two years). Primary and secondary stem numbers are combined. (nd = no data).

SPECIES	TREE HEIGHT CLASS					
	<0.5		0.5-1.5		1.5-2.5	
	2 months - 2yrs	1-2yrs	2 months - 2yrs	1-2yrs	2 months - 2yrs	1-2yrs
<i>A.karoo</i>	0.59	0.25 (8)	0.81	0.5 (12)	0.77	0.43 (10)
<i>A.nilotica</i>	0.70	0.46 (10)	0.80	0.70 (10)	Nd	nd
<i>A.caffra</i>	nd	nd	0.69	0.60 (9)	0.77	0.66 (11)
<i>D.cinerea</i>	0.36	0.55 (10)	0.52	0.35 (10)	0.12	0.21 (10)

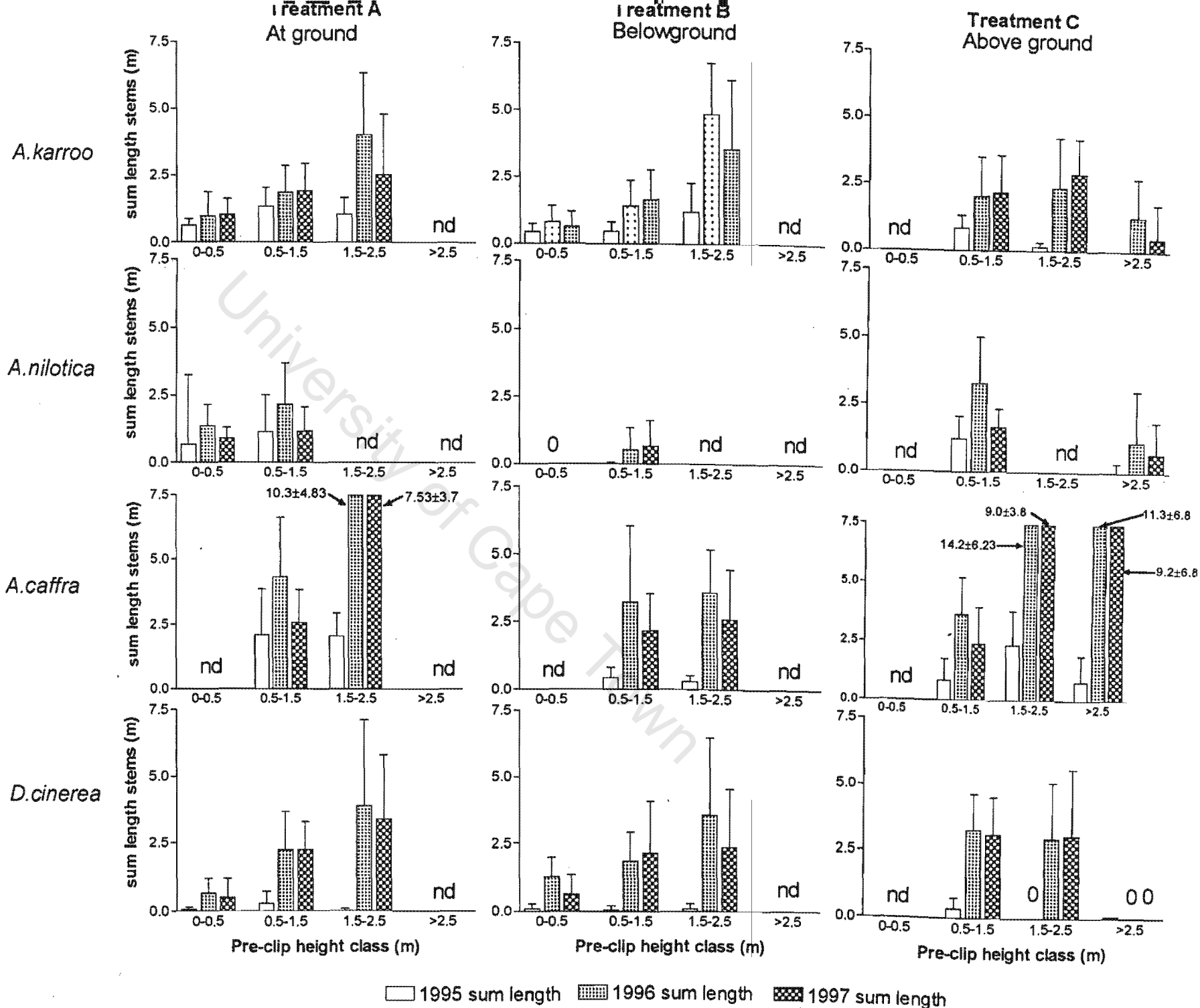
2.5.2.3 Sum of the length of all resprouting stems

Figure 2.6 shows the mean sum of the length of all resprouting stems for each species, clipping treatment and across four height classes. Measurements were recorded only for regrowth and not for pre-clipped individuals. The sum of the length of all resprouting stems increased in the first year of growth following clipping. In the second year following clipping, species varied in the sum of the length of all resprouting stems, either decreasing or remaining unchanged. *A.karoo* showed the highest regrowth vigour, with very little difference in response between the different clipping treatments. Trees in the 0.5-1.5m height class had the highest regrowth rate in *A.karoo*.

In *A.nilotica* clipping treatment B had the most obvious effect in causing a lower regrowth response. Following clipping treatment C, trees in the 0.5-1.5m height class showed slightly higher regrowth vigour than those following clipping treatment A because a greater number of resprouting stems were produced. The >2.5m height class showed very low regrowth vigour.

In *A.caffra* clipping treatment B reduced regrowth in the 1.5-2.5m height class. Clipping treatment C showed greater regrowth than clipping treatment A for 1.5-2.5m height class. The 1.5-2.5m and >2.5m were the most vigorous of all the height classes.

Figure 2.6 Mean sum (and standard deviation) of the lengths of resprouting stems produced after clipping. Measurements recorded 3 months (1995), 1 year (1996) and 2 years (1997) after clipping. Illustrated here for the three clipping treatments, four species and four height classes. (nd = no data collected; 0 = all dead).



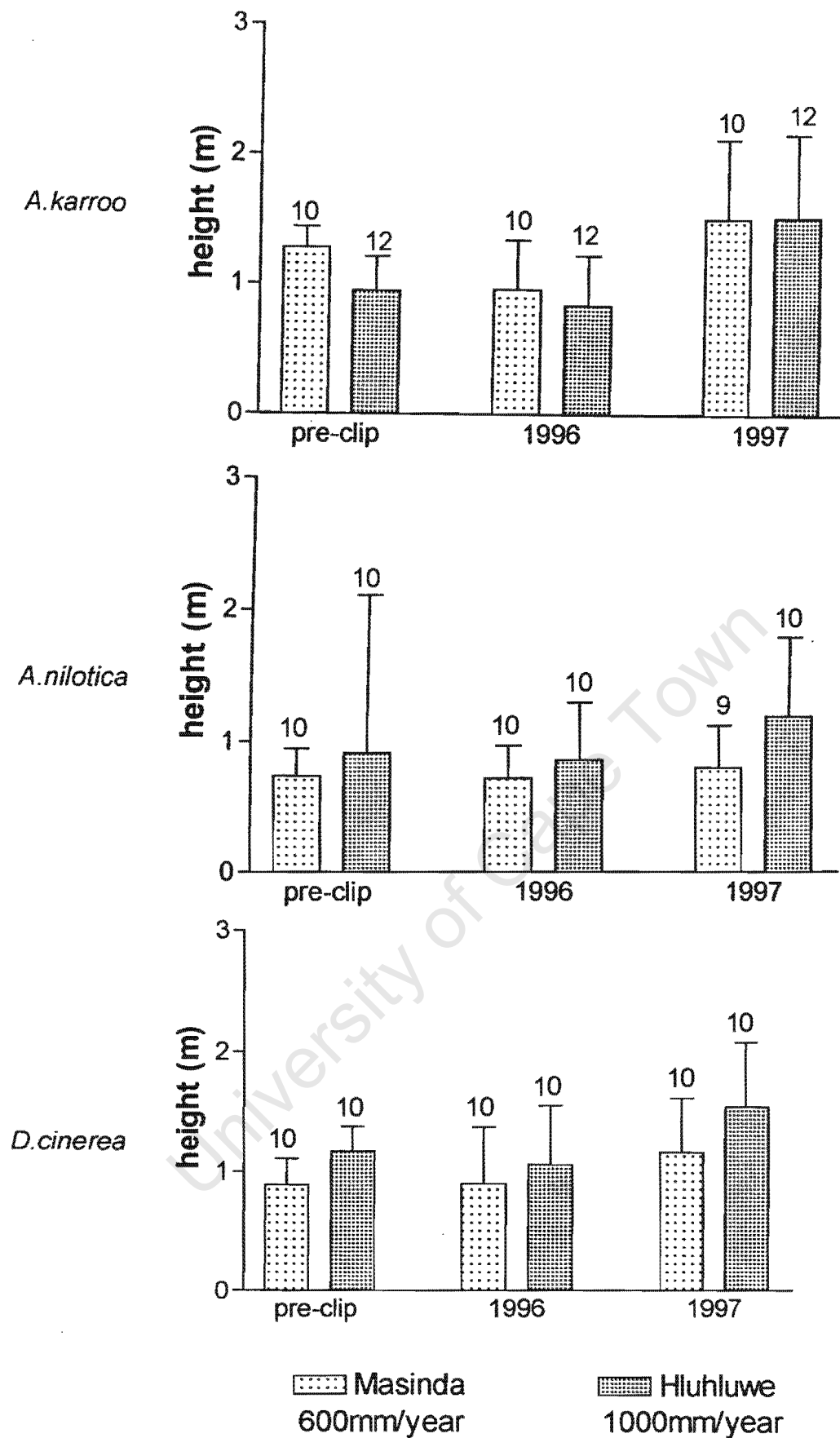


Figure 2.7.1 Comparison of tree response in terms of mean height growth (and standard deviation) in *A.karoo*, *A.nilotica* and *D.cinerea* at high and low rainfall (Masinda m.a.r. approx. 650mm and Hluhluwe approx. 1000mm).

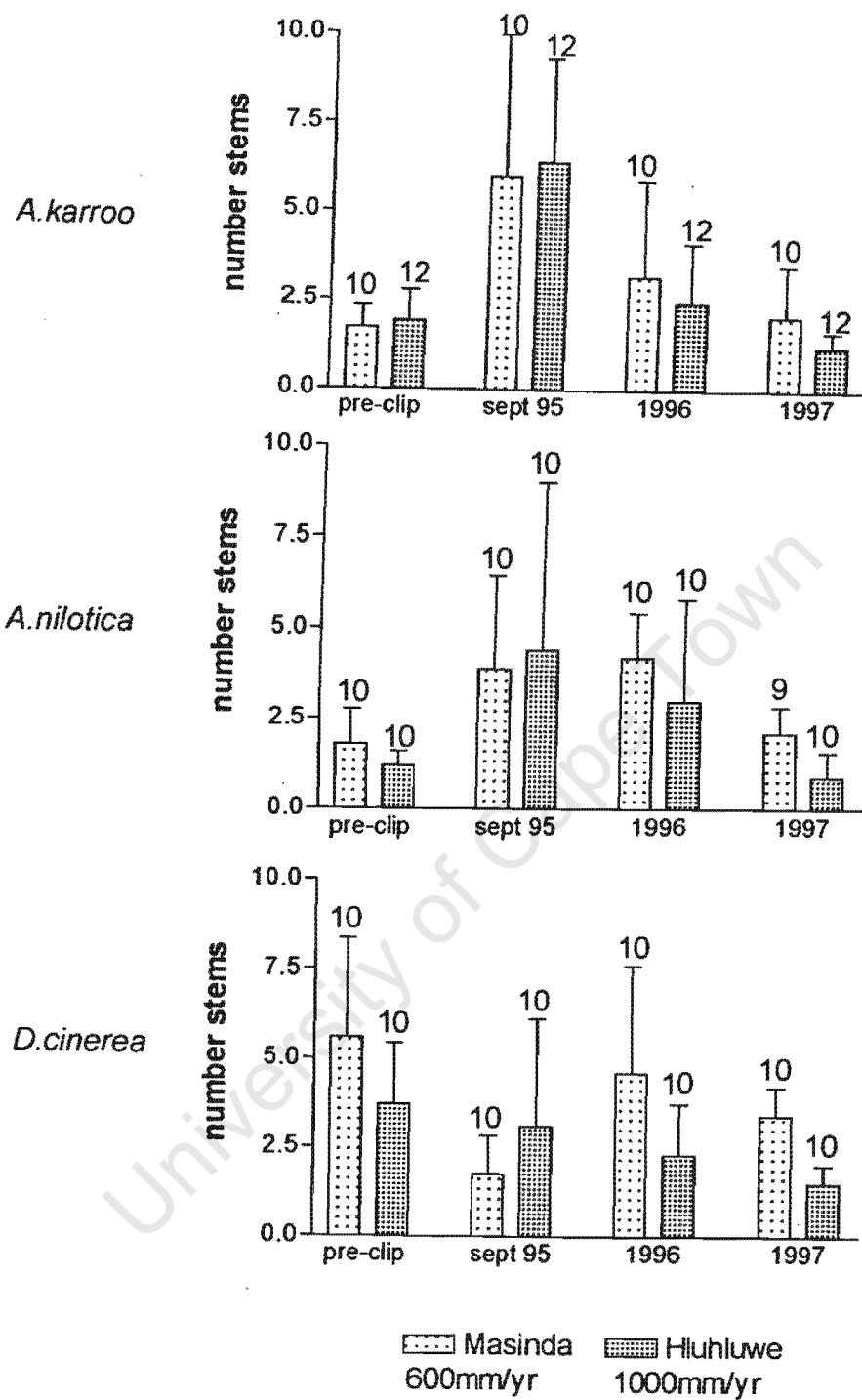


Figure 2.7.2 Comparison of tree response in terms of the mean number of resprouting stems (and standard deviation) in *A.karoo*, *A.nilotica* and *D.cinerea* at high and low rainfall (Masinda m.a.r. approx. 650mm and Hluhluwe approx. 1000mm).

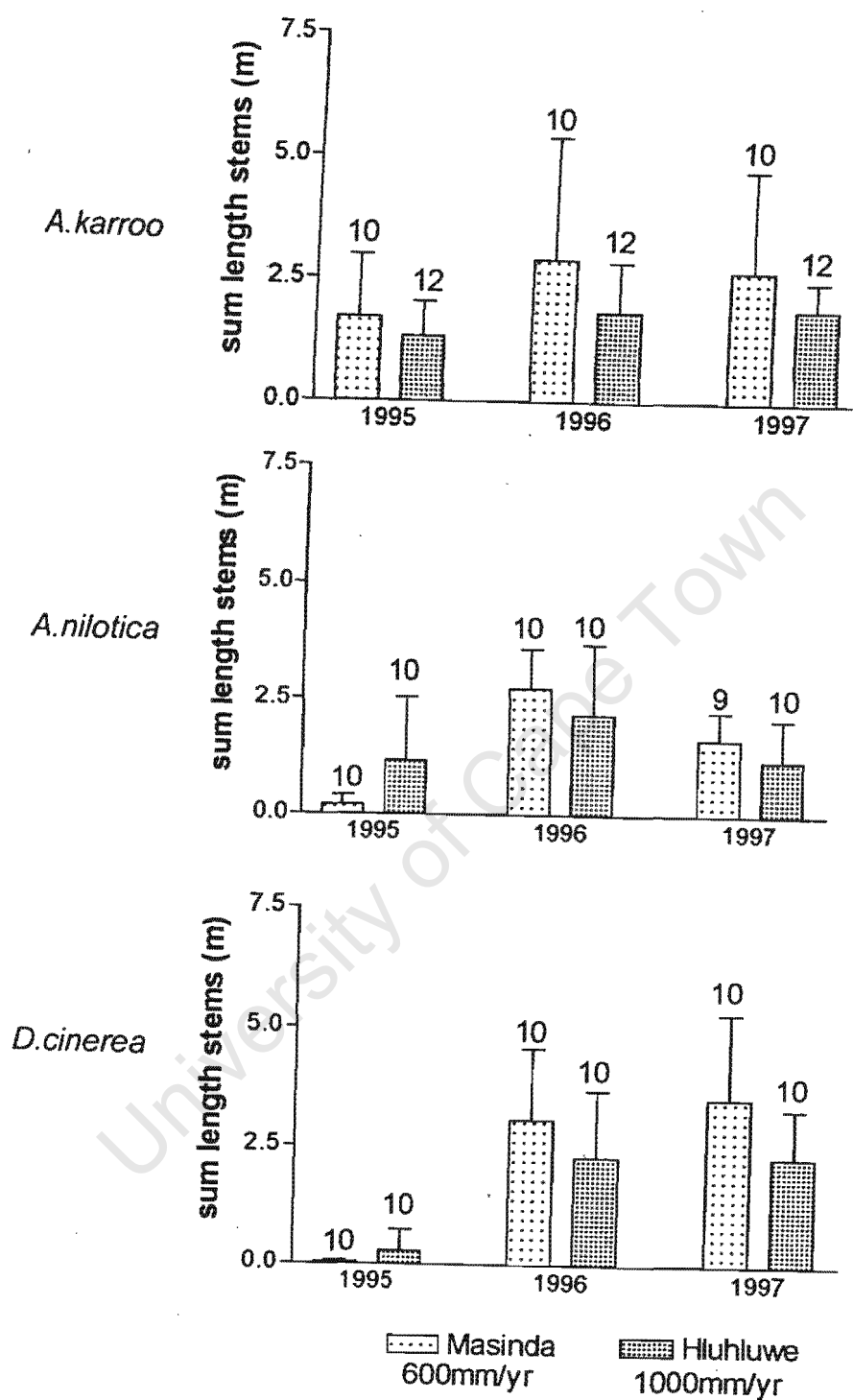


Figure 2.7.3 Comparison of tree response in terms of the mean sum of the length of resprouting stems (and standard deviation) in *A.karoo*, *A.nilotica* and *D.cinerea* at high and low rainfall (Masinda m.a.r. approx. 650mm and Hluhluwe approx. 1000mm).

D.cinerea showed no differences across clipping treatments or height classes in regrowth vigour. *D.cinerea* showed an initial lag in regrowth compared to the three acacias because of inherent phenological differences between the species.

2.5.2.4 Response of trees to clipping at a low versus high rainfall sites

Figures 2.7.1-2.7.3 compare regrowth height, number of resprouting stems and sum of the length of resprouting stems in *A.karoo*, *A.nilotica* and *D.cinerea* at two sites with different rainfall. *A.caffra* was absent from the arid site. No tree mortality was recorded at the arid site. The response of trees to injury at lower rainfall did not differ substantially from that at higher rainfall in the first year following clipping. However, in the second year, the growth rate slowed down in *A.karoo* and *A.nilotica* suggesting a switch from growth subsidised from stored carbon to growth based on current foliage.

2.6 Discussion

2.6.1 Resprouting ability

The four study species exhibited developmental changes in sprouting ability. All species had the ability to resprout at a very early age (6 months). This sprouting ability is retained and improved with tree height, until maturity, when sprouting ability rapidly declines, with *A.caffra* adults being the only exception (Figure 2.3). The variation in number of resprouting stems across height classes as well as species is indicative of the bud dynamics and or energy reserve status of the trees. Species vary in location and size of bud banks suggesting two generalized life history types described later. Variation in patterns of regrowth vigour may be a key for understanding savanna system dynamics better and in turn aid management.

2.6.1.1 Height dependent survival

In all four study species mortality following clipping was generally greatest in seedlings and mature trees. Six month old seedlings of all four study species show approximately 50% survival following clipping at ground level showing that the ability to resprout is

acquired at a very early age (Figure 2.3). The fact that mortality was relatively high in seedlings suggests they lack meristems and or carbon reserves to replace the lost tissue.

Trees in the intermediate height classes in this study are highly resilient to injury. In some species (e.g. *A.nilotica*) only extensive damage to the root crown caused mortality and it is unlikely that such severe damage to the root crown would occur naturally.

Trees >2.5m exhibited higher mortality rates than intermediate height trees. *D.cinerea* trees >2.5m (mostly single-stemmed individuals prior to clipping) did not resprout following clipping. However, this response may be limited to the form of *D.cinerea* present in HUP. A different form of *D.cinerea*, occurring north of the HUP, is a multi-stemmed at >2.5m (e.g. Mkuze Game Reserve) and resprouts vigourously after fire (Goodman pers comm). Large trees of *A.karoo* and *A.nilotica* show a reduced sprouting ability. *A.nilotica* showed the highest mortality rates of all species in this clipping experiment. Loss of resprouting ability in larger trees may be due to fewer buds, too thick bark or to reduced carbon reserves in roots of mature trees. Although no mortality was observed in *A.caffra* except at the seedling stage, the seedling mortality was higher than in the other species. *A.caffra* was followed by *A.karoo* in tolerance to injury. Thus, once *A.caffra* and *A.karoo* are established they are highly resilient to injury.

The low rate of mortality in larger trees of *A.caffra* indicates that they are persistent features in the landscape in the face of frequent disturbance, relative to the other study species. *A.caffra* is thus a typical example of a species where individuals are highly persistent through retention of sprouting ability in adults. Persistence through sprouting is thought to be associated with poor seedling establishment (Bond 1997; Kruger *et al.* 1997) due to the associated trade-offs. In *A.caffra* the low number of seedlings and juveniles in the population relative to the number of adults, as well as the low seedling survival rate found in this study suggest that these trade-offs exist.

2.6.1.2 Location of buds and size of bud banks

The location of sprouts depends on the location of living meristematic tissue (buds) as well as bark thickness. Thick bark appears to act as a barrier inhibiting shoot development. In

most cases resprouting stems originated from the highest point subtending the cut line. Clipping treatment C (at 10cm above ground) provides a good indication of the differences in bud location and regrowth strategies between species and across height classes. Following clipping treatment C, I expected resprouting stems to originate predominantly from the stem, but this was not the case for some *A.karoo* and *D.cinerea* individuals, which resprouted from the root crown as well. This can probably be attributed to either the loss of epicormic buds or to a barrier effect imposed by thicker bark in taller trees. *A.nilotica* showed a different pattern, having less capability of sprouting from the root crown than the other species, which suggests that there are relatively few buds seated in the root crown. This may be because *A.nilotica* has thick bark to protect epicormic buds during fire. *A.karoo* has thinner, less protective bark, and trees have to grow quickly to reach escape height, so buds may be better placed in root crown and on the stem. *A.karoo* produced the fewest number of resprouting stems following clipping treatment C possibly due to effects of apical dominance. In *D.cinerea*, resprouting stems originate predominantly from the crown, suggesting together with thin bark, that there are very few buds located on the stem. *A.caffra* produced many resprouting stems, with multiple dominant stems which are maintained as the tree matures and give the tree a cage-like growth form.

It is important to note the difference within and between species in absolute numbers of resprouting stems produced following each clipping treatment. The number of sprouts is an indication of the size of the bud bank. The three clipping treatments show differences in bud locations between species and across height classes.

It is expected that *A.nilotica* and *A.caffra* will resprout epicormically more frequently than the other two species which are more frequently topkilled. This is a bark thickness constraint as opposed to a bud availability argument since thicker bark on the stems insulates epicormic buds from the heat of the fire.

2.6.2 Resprouting vigour - The ecological implications of different resprouting strategies

2.6.2.1 Height recovery

Savanna trees have to be resilient to injury due to the frequency of fire and herbivory in their environment. The tree species in this study, like most other savanna trees, are potent resprouters. But what makes these trees so resilient to injury and how do resilience strategies vary? The seedling and intermediate sized trees are the most notably affected by injury, falling within the flame and browse zone. In this study, not only do the intermediate height trees have the lowest mortality rates but also, to varying degrees, they have very high regrowth rates following injury relative to seedlings and mature trees.

The vigour of height regrowth, shown in Figures 2.5.1-2.5.3, shows that most trees in the study can equal or increase their pre-clip height rapidly (in cases within one year of injury). Further, this regrowth ability was strongly related to pre-clip height. In *A.karoo* and *D.cinerea* the 0.5-1.5m height class was most vigorous in regaining and exceeding pre-clip height. Unfortunately there were no *A.nilotica* trees present in this height class. *A.karoo* and *D.cinerea* trees greater than about 1.5m showed a decline in resprouting height growth most likely due to lower carbon reserves or fewer buds available. *A.caffra* has the fastest regrowth rate.

The fact that response of trees at lower and higher rainfall did not differ appreciably suggests that regrowth rates were independent of moisture availability, but rather were a function of pre-clip height. This is consistent with the idea that tree recovery in the first year after clipping or burning is related to stored reserves whereas subsequent growth depends on current photosynthesis under prevailing environmental conditions.

Information on the rate of height regrowth is critical for predicting the time taken for a tree to escape the flame zone. There are at least two possible alternate strategies trees display for surviving the flame zone or escaping to become "adults". These strategies are illustrated and discussed in greater detail in Chapter 5. Trollope and Tainton (1986)

and Trollope (1998) showed that *A.karoo* in Eastern Cape bushveld reaches escape height at 2.5m (i.e. height at which topkill avoided). However this should vary for different species. Bark thickness may be the main factor in explaining any difference in average topkill heights and is investigated in the following chapter.

Figure 2.8 is a summary of tree response to clipping and shows how some trees reverted to shorter height classes following clipping. The diagram shows lumped response across all clipping treatments. This data could be explored further using a matrix model.

In order to survive injury of their aerial parts by either having thick insulating bark and epicormic bud banks or resprouting from the root crown, trees require an energy reserve. The sum of the length of all resprouting stems is a surrogate for the stored energy available to a plant for regrowth in the first season since injury. The results show that a large amount of resources are allocated to growth in the first year following injury, but in the second year I hypothesise that growth rates rapidly decline as growth is based on current photosynthesis.

A.karoo, and to a greater extent *A.nilotica*, have to escape the flame zone at some stage in their lives if they are to become reproductively mature, since few trees within the flame zone were found to have flowers. They grow to escape the flame zone by gradually accumulating carbon stores in the roots (see Chapter 5, Figure 5.1) from fire to fire until there is a window for recruitment out of the flame zone. This recruitment window could be either a break in the fire frequency, a series of less intense fires (i.e. lower levels of topkill), or gradual accumulation of sufficient reserves to grow above the flame height under the prevailing fire regime. From the results presented on regrowth rates (Figure 2.5.1), it is clear that trees can recover their pre-clip height within one year after which growth rates drop off rapidly. The results presented in Chapter 4 show that *A.karoo* and *A.nilotica* trees have very high concentrations of carbon in their roots when they are intermediate sized (i.e. gullivers).

Alternatively non-gulliver species that remain multi-stemmed through their lives such as *D.cinerea* and *A.caffra*, do not vary much in their carbon reserves with height. The only exceptions are single stemmed adults of *D.cinerea* in HUP which have very low carbon reserves. *D.cinerea* and *A.caffra* do not necessarily need to escape the flame zone since they are able to reproduce within it. They are highly multi-stemmed through to adulthood

(especially *A.caffra*). The frequency of flowering among shorter or juvenile, more multi-stemmed individuals is much greater in these non-gulliver species (Bond *et al.* in press).

A general rule that requires testing for other species is that the mean number of resprouting stems in mature plants is a predictor of gulliver versus non-gulliver life history types. In this study the mean number of resprouting stems in the two non-gulliver type species (*A.caffra* and *D.cinerea*) was greater than in the gulliver type (*A.karoo* and *A.nilotica*).

2.6.2.2 Rates of self thinning in resprouting stems

The number of resprouting stems in both gulliver and non-gulliver type species decreases with time since clipping. Mean rates of decline in Table 2.4 show that there are two distinct classes of stem thinning. In the gulliver type species (*A.karoo* and *A.nilotica*) there was a greater overall rate of stem thinning with time than in the non-gulliver type species (i.e. *A.caffra* and *D.cinerea*) (Table 2.4 and Figure 2.4). One would expect a gulliver to tend towards single stemmedness as it approaches escape height, and in non-gullivers, for the number of resprouting stems to increase or stay constant with increasing height classes. Trees in the largest height class, except in *A.caffra* show, a decline in number of resprouting stems with increasing height. *A.caffra* maintains relatively high stem numbers at higher height classes. The alternative non-gulliver strategy is to remain in the fire zone as multi-stemmed trees such as *D.cinerea* and *A.caffra*.

The decrease in number of resprouting stems can in most cases be attributed to die-off of the secondary stems (these were frequently observed as dead) (Table 2.3). Secondary stems may serve to maximize the photosynthetic surface area for rapid carbon gain in order to replenish reserves before the next fire. The juvenile type foliage produced after defoliation in a wide variety of taxonomically unrelated resprouting shrubs has very high photosynthetic capacity. In Mediterranean shrublands species, change in chloroplast structure and an increase in the concentration of chlorophyll have also been recorded (Christodoulakis *et al.* 1986). Some of these mechanisms may be present in, and contribute to, the relative resprouting success in resprouting savanna shrubs and trees. This may be an area worthy of future research attention and could be verified

quantitatively by removing secondary stems and monitoring regrowth rates. The young tender resprouting stems are heavily browsed and this may be another reason for the great number of resprouting stems produced. This could be investigated by protecting trees from browse.

Although the number of resprouting stems decreases in the second year's growth, there was an overall increase in the biomass allocated to resprouting stems, as reflected by the sum of length of resprouting stems (Figure 2.6). As trees approach escape height, it is expected, in gullivers such as *A.karoo*, that one stem will become a dominant pole. This was observed in *A.karoo* in the field and could be quantified by analysing ratios of resprouting stem lengths in trees.

Limitations in the data for some species was a shortcoming in this study, especially in *A.nilotica* where the response of trees in the 1.5-2.5m height class would have been very informative. In the case of the seedlings, some of the sample sizes were too small due to poor seedling germination and establishment.

In the following chapter, results from clipped trees will be compared with that collected from trees following controlled burns in the HUP.

SPECIES	SIZE/HEIGHT CLASS (m)					
	SEEDLINGS	<0.5	0.5-1.5	1.5-2.5	>2.5	
<i>A.karoo</i>	↻ ↓ 55%	↻ ↓ 2%	↻ ↓ 1%			↓ 70%
<i>A.nilotica</i>	↻ ↓ 40%	↻ ↓ 50%	↻ ↓ 20%	×		↓ 71%
<i>A.caffra</i>	↻ ↓ 50%	×	↻	↻		↓ 1%
<i>D.cinerea</i>	↻ ↓ 50%	↻ ↓ 15%	↻ ↓ 3%	↻ ↓ 10%		↓ 100%

↻ = trees re-grew to pre-clip size/height class

↓ = % mortality

× = no trees sampled in size class

Figure 2.8 Summary of regrowth and mortality for four study species following clipping. Response is combined for all clipping treatments. Percentage mortality is indicated and X = number of trees sampled in that particular height class.

2.7 Conclusion

Trees are highly resilient to injury and exhibit marked differences in response to injury both within and between species. All four study species have the ability to resprout at a very early age (i.e. at 6 months) with a 50% success rate. Sprouting ability was retained and improved with tree height, until maturity when sprouting ability rapidly declines, with *A.caffra* adults being the only exception in that trees retain resprouting ability through to adulthood. Resprouting vigour followed a similar size dependent pattern but the regrowth rates differed among species. The factors most likely responsible for sprouting in trees are the availability of buds and carbon reserves.

From these patterns, two distinct life histories distinguish the species in this study. *A.nilotica* and *A.karoo* display typical gulliver type life histories (after Bond and Van Wilgen 1996) where juveniles start as multi-stemmed and eventually emerge from the fire zone as single stemmed trees. Adults lose their sprouting ability. The selective forces of frequent burning in the mesic savannas of KwaZulu Natal, may have selected for the unique spindle form *A.karoo* that is highly resilient to injury. The non-gulliver type species, *A.caffra* and *D.cinerea*, survive to maturity within the flame zone, and remain multi-stemmed throughout. *A.caffra* retains vigorous sprouting ability when mature whereas *D.cinerea* loses this ability. Multi-stemmedness in adult trees may be a clue for distinguishing the gulliver versus non-gulliver life-history and should be further tested in other species and systems.

These life history differences provide useful insights into understanding savanna functioning at the level of the individual and have important implications for management that are discussed in Chapter 6 (i.e. height dependent survival curves).

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3 RESPONSE OF ACACIA KARROO, ACACIA NILOTICA AND DICHROSTACHYS CINEREA TO FIRE

3.1 Introduction

This chapter deals with the response of *Acacia karroo*, *A. nilotica* and *Dichrostachys cinerea* to controlled burns of different intensity and season. Specific responses investigated include mortality, topkill and regrowth rates, across a range of tree heights. The introductory section in Chapter 2 dealing with response of savanna trees to injury also serves to introduce this chapter.

Although it is widely believed that the effect of fire on savanna trees is dependent on fire intensity, there remains a lack of understanding on both the behaviour of fires and the plant response to variation in fires.

The behaviour and characteristics of different types of fires is a complex subject and is not elaborated on here, but has been covered in detail by several authors (e.g. Beaufait 1965; Vines 1980; Trollope 1984; Trollope and Potgieter 1985; Whelan 1995). This study makes use of fire intensity as a basis on which to evaluate tree response following fire. Fire intensity is a measure of how fiercely a fire burns and is usually estimated indirectly by using Byram's (1959) fireline intensity equation;

$$I = HWR$$

where I is the fireline intensity ($\text{kJ s}^{-1} \text{m}^{-1}$), H is the heat yield of the fuel (kJ kg^{-1}), W is the mass of fuel consumed (kg m^{-2}) and R is the rate of spread of the fire (ms^{-1}). H is generally assumed to be a constant at 890 kJ kg^{-1} for grass material burning in grassland and savanna areas (Trollope 1983) this is a generally accepted constant since H does not vary much between species. However R and W can vary greatly between fires (Bond and van Wilgen 1996). Because fire intensity is sensitive to factors such as fuel properties (amount, composition, moisture content) and climate condition (wind, RH, ambient temperature) as well as topography, it is often very difficult to predict before the fact. Fire intensity values of

200-6000kJ/s/m have been recorded for savannas in southern Africa (Trollope 1984; Van Wilgen and Wills 1988).

Although fire intensity has received more research attention in savannas relative to season of burn, the use of fire intensity as a management tool has not always been based on a clear understanding of tree response to injury. Many rangeland and reserve managers in KwaZulu Natal and elsewhere in South Africa consider very high intensity burns as optimal for controlling dense woody thickets, believing that fire intensity correlates positively with tree mortality. However, available research findings do not necessarily support this notion (Rutherford 1983; Hodgkinson 1998; Trollope 1980; Trollope *et al.* 1995; Trollope 1998). Recent work in Australia (Hodgkinson 1991, 1998) has shown that even for great increases in fire intensity there is no significant increase in tree mortality. In South African savannas Trollope (1980, 1984, 1998) found that high intensity fires caused very little tree mortality, even under the hottest burns. Thus once the above ground parts of a tree are killed by fire (i.e. "topkill" is achieved), any further increase in fire intensity may have a negligible effect on tree mortality.

Tree mortality usually occurs in a small proportion of a population of burnt savanna trees (Frost 1984). On the whole trees are more likely to resprout in a variety of ways and at different rates. Different species attributes may potentially play a role in this (i.e. bark thickness determines the degree to which buds are protected from heat (Ryan and Reinhardt 1988)). Fire intensity may also affect regrowth rates of topkilled trees. In some cases variation in fire intensity has been shown to correspond with vegetative recovery (Trollope 1984; Trollope and Tainton 1986; Trollope *et al.* 1995; reviewed in Bond 1997) but research has focussed mainly on the grass and herbaceous component (Trollope *et al.* 1989).

Other researchers claim that fire intensity is not necessarily a good predictor of biological effects (Alexander 1982), but consider flame height to be better since it determines topkill (Van Wilgen and Wills 1988) (i.e. flame height and fire intensity may not always be positively correlated). However, whether fire intensity or flame height is the key factor, our knowledge on variation of tree response to fire is poor. This is because very few studies have investigated response at the level of individual trees, but rather the focus has been on responses at the system level.

In this study I investigated whether fire intensity played a role in tree response and if so what the biological effects of fire intensity were (e.g. fire intensity may influence topkill which may depend on species characteristics). Tree response to fire season may vary depending on the state of carbon reserves at the time of the fire, the length of the growing season subsequent to burning or possibly just the interaction between season and fire intensity (to a degree determined by fuel load). Although this chapter includes fires in different seasons, the specific role of fire season will be dealt with in Chapter 4.

3.2 Aim of this study

This study investigates variation in mortality, topkill and regrowth in *A.karoo*, *A.nilotica* and *D.cinerea* following eight controlled burns of varying intensity and season. Variation within (across a range of tree heights) and between species is investigated. Tree response following these fires is also compared with response found following clipping experiments in Chapter 2. The biological basis for inter- and intraspecific variation in resprouting potential was investigated by looking at variation in bark thickness. Other biological attributes affecting survival include carbon storage in roots and the location of viable bud banks, however this was beyond the scope of the project and deductions are made based on the carbohydrate results found in Chapter 4.

The observed response of trees is compared with that predicted by models developed by Higgins *et al.* (2000) that estimate probabilities of topkill and resprouting.

3.3 Methods

3.3.1 Study Area

For a general description of the study area see Chapter 1. Choice of study sites was limited to areas being burnt in the year of the study (Photos 9-12). Sites chosen resembled those chosen for the clipping experiments in terms of community composition, time since last burn, rainfall and soil type. One site, Masendwini R, had been burnt the previous year to

this study. In total eight controlled burns were assessed during 1995-1996 (see Chapter 1, Figure 1.2).

3.3.2 Fire intensity measurement

In order to determine the intensity of the controlled burns in this study, detailed measurements were made before and during each fire (Table 3.1). It was not always possible to collect all information necessary (e.g. rate of fire spread) to calculate fire intensity according to Byram's (1959) physical fire equation $I = HWR$, therefore an alternative fire intensity model developed by Trollope (1998) was used to estimate fire intensity (equation 1). In this model the realised fire intensity is dependent on the fuel load present, the fuel moisture content, the relative humidity, and the wind-speed on the day of the fire. The multiple regression model for predicting fire intensity is:

$$FI = 2729 + 0.8684 y - 530\sqrt{x} - 0.907 RH^2 - 596/W \quad (1)$$

Where FI = fire intensity kJ/s/m; y = fuel load kg/ha; x = fuel moisture %; RH = relative humidity %; W = wind speed m/s.

This statistical model was developed using 200 monitored fires in South African savannas ($p < 0.01$, d.f.=196, $R^2=0.60$, Trollope 1998). Trollope (1998) tested the model against independent fire behaviour data and it accounted for 56 % of the variation in fire intensity.

3.3.2.1 Estimating fuel load

Fuel load is one of the most important factors influencing fire intensity (Trollope 1998) and in savannas is based on the amount of grass biomass. *Themeda triandra* and *Cymbopogon excavatus* were the dominant fuel types in all controlled burn areas in this study and in some areas of the HUP, occur in very tall and dense stands. Fuel loads were estimated prior to each fire using a disc pasture meter technique developed by Bransby and Tainton (1977). The disc pasture meter has not yet been calibrated for the HUP therefore estimates of fuel loads are made based on the Eastern Cape thornveld calibration of Trollope (1983) which most closely matches the conditions at HUP, but has a lower grass biomass. Fuel load is predicted by the following regression equation:

$$y = 340 + 388.3x$$

(2)

where y = mean fuel load kg/ha

and x = mean disc height cm

The fuel loads calculated for each site are presented in Table 3.1.

3.3.2.2 Fuel moisture content

Fuel moisture is an important factor in determining the intensity of a fire by affecting the ease of ignition, quantity of fuel consumed and the combustion rate of the different types of fuel. The moisture released from fuel during burning has a smothering effect by reducing the oxygen near the burning material. Fuel moisture content was determined for grass samples collected immediately prior to burning. Samples were weighed then dried and % fuel moisture calculated. Fuel moisture for each burn site is presented in Table 3.1.

3.3.3 Tree response following fire

Response of individual trees following the eight controlled burns was recorded in July 1997, 11 months after the six winter fires and six months after the two summer fires. Both pre-fire and regrowth heights were measured in randomly selected trees following each controlled burn in either 10 x 10m plots or in transects. The samples reflected species composition and height classes in the field and resulted in sample sizes of some species and height classes being too low to be analyzed in some cases. For this reason *A.caffra* was omitted from this study. Plot and transect data was combined for the data analysis. Additional regrowth measurements were made for the Zinquimeni summer burn in August 1998 (i.e. 18 months post clip), however by this time the pre-burn stems had broken off, restricting the comparison of tree regrowth between summer and winter burns.

For each tree, pre-fire height was estimated from the tallest scorched stems which persist until the next burn in all trees except the shortest ones. Thus this method was effective for pre-fire heights > 0.5m. Plants smaller than 0.5m pre-fire stems are mostly

consumed in the fire and this results in underestimates of percentages topkill and mortality. For the purposes of this study all trees with no pre-fire stem were assumed to have pre-fire heights <0.5m. For each individual, regrowth height was measured as well as whether or not the individual was topkilled (i.e. all above ground parts killed) or dead (i.e. all above and below ground parts killed). Trees that had been topkilled and had not resprouted 11 months post burn were assumed to be dead. The number of stems and length of all stems was not recorded as was done in the clipping experiment in Chapter 2. It was possible to estimate the pre-fire height of non-topkilled trees from fire scorching scars on the stems.

3.3.4 Bark thickness

Bark thickness is thought to play a major role in affecting topkill in trees. Thicker bark insulates tree stems and may therefore reduce levels of topkill. Data on bark thickness were collected from trees used in the clipping experiment in Chapter 2. Bark thickness was recorded from the tallest stem in trees clipped at 10cm above ground, in four tree species and over a range of height classes. Bark thickness was measured with callipers at the average point of thickness.

3.3.5 Data analysis

The effect of fire intensity on levels of topkill in a stand, tree mortality and regrowth vigour was explored across species and a range of tree heights. Data were analysed using XY plots, linear regression analysis, analysis of variance and chi-square (STATISTICA). Homogeneity of variances of proportion regrowth and pre-fire height was tested using Bartlett Chi-square. The effect of fire season on topkill and mortality was also investigated for two fires. The average height of trees that escaped topkill was calculated to determine whether levels of topkill and tree escape are based on the effects of different species, the patchiness of fire or whether fire is selective on tree height.

To determine if bark thickness correlates with % topkill, a regression analysis for bark thickness and tree height was performed.

I tested two models of Higgins *et al.* (2000) which predict the frequency of escape from gullivers to mature trees, by simulating how fire intensity and tree size influence the likelihood of topkill (equation 3). For equation 3 I plotted expected and observed responses.

Higgins *et al.* (2000) predict topkill by the following equation:

$$p_t = \frac{\exp(4.3 - 5.003 \ln(h) + 0.004408 \sqrt{Q})}{1 + \exp(4.3 - 5.003 \ln(h) + 0.004408 \sqrt{Q})} \quad (3)$$

Here p_t is the probability of topkill; h is stem height (m) and Q is the fire intensity ($\text{kJ.s}^{-1}.\text{m}^{-1}$). This equation is derived from field measurements collected by Trollope (1998).

3.4 Results

3.4.1 Fire intensity measurements

Fire intensity measurements and fuel characteristics are presented in Table 3.1 for the eight controlled burns studied. In some cases it was not possible to collect all pre-fire data, however this did not affect the calculation of fire intensity according to equation 1. Fire intensity ranged from 650-5900 kJ/s/m , with most fires being classified as very hot according to Trollope (1998). These results also fall within the range found by van Wilgen and Wills (1988) who found intensities of 194-5993 kJ/s/m in ten experimental burns in northern Natal. Van Wilgen and Wills (1988) found the mean fuel load to be 3800 kg/ha , which is at the lowest end of the fuel load range found in this study. This suggests that the Eastern Cape calibration of the disc pasture meter used in this study may have produced overestimates of fuel loads in HUP.

3.4.2 Tree response

3.4.2.1 Species abundance

Across all eight study sites a total of 1512 trees were sampled in which the overall ratio of species was approximately 7 *A.karoo* : 3.5 *D.cinerea* : 1 *A.nilotica*. This ratio varied at each burn site, however *A.nilotica* was always least abundant relative to *A.karoo*.

D.cinerea varied in relative abundance between sites. At five out of the eight sites *A.karoo* was numerically dominant. Appendix 3.1 contains details on the total number of trees sampled per fire and height class, together with number and percent that were topkilled and percent that were dead following the controlled burns.

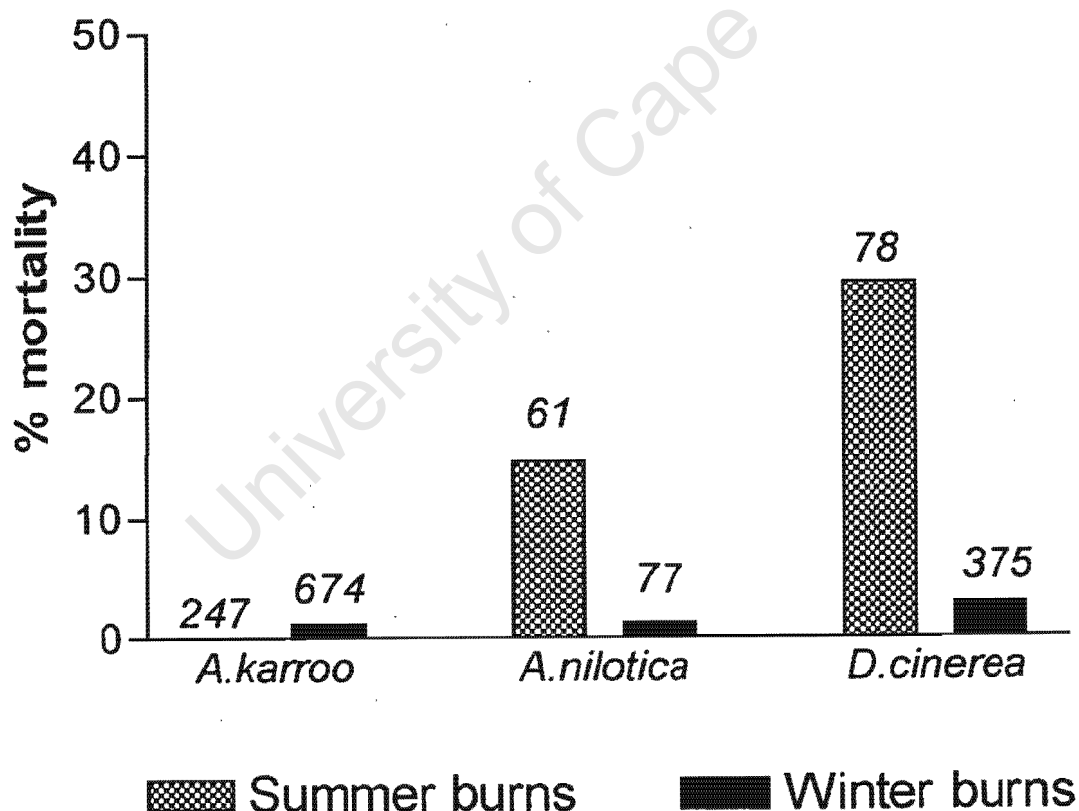


Figure 3.1 Tree mortality (%) following two summer burns and six winter burns in the HUP. Number of trees sampled is indicated above the bars.

Table 3.1 Fire characteristics and intensity. Fuel load calculated using equation 2 and intensity calculated using equation 1. nd = no data available

FIRE CHARACTERISTICS	SITE NAME							
	Magangeni winter	Zidonini winter	Masendwini R winter	Masendwini L winter	Zinquimeni winter	Zinquimeni summer	Gontshi winter	Umfolozu summer
Date of fire	9/95	9/95	9/95	10/95	10/95	1/96	9/95	3/96
Time of day	14h20	9h50	9h30	15h25	nd	nd	12h00	12h30
Wind direction	W	E	NE	SE	nd	nd	nd	S
Avg wind speed (m/s)	8	0.5	7	2.5	4.5	1.5	5.4	4.5
Air temperature (°C)	24	25	27	24	23	30	23	34
Relative humidity (%)	53	17.6	60	60	20	65	24	70
Flame height (m)	2.5	1.5	3	3.5	nd	nd	nd	nd
Flame velocity (m/s)	0.6	0.08	nd	0.56	nd	nd	nd	nd
Type fire back/head	H	H	B	H	H	H	H	H
Average grass height (m)	0.8	nd	0.8	0.6	nd	nd	nd	0.8
Average disc pasture meter readings (cm)	18.1	8.5	12.6	15.0	9.1	14.8	17.2	31.5
Fuel load (kg/ha) ²	7368	3644	5248	6176	3874	6083	6999	12579
Fuel moisture (%)	7.7	20.7	10.9	8.1	15.3	35.0	18.4	41.6
Fire intensity kJ/s/m¹	5000	2000	2200	3100	3500	650	5900	5700
Intensity category (After Trollope 1998)	VERY HOT	HOT	HOT	VERY HOT	VERY HOT	COOL	VERY HOT	VERY HOT

¹ estimated from equation 1; ² estimated from equation 2.

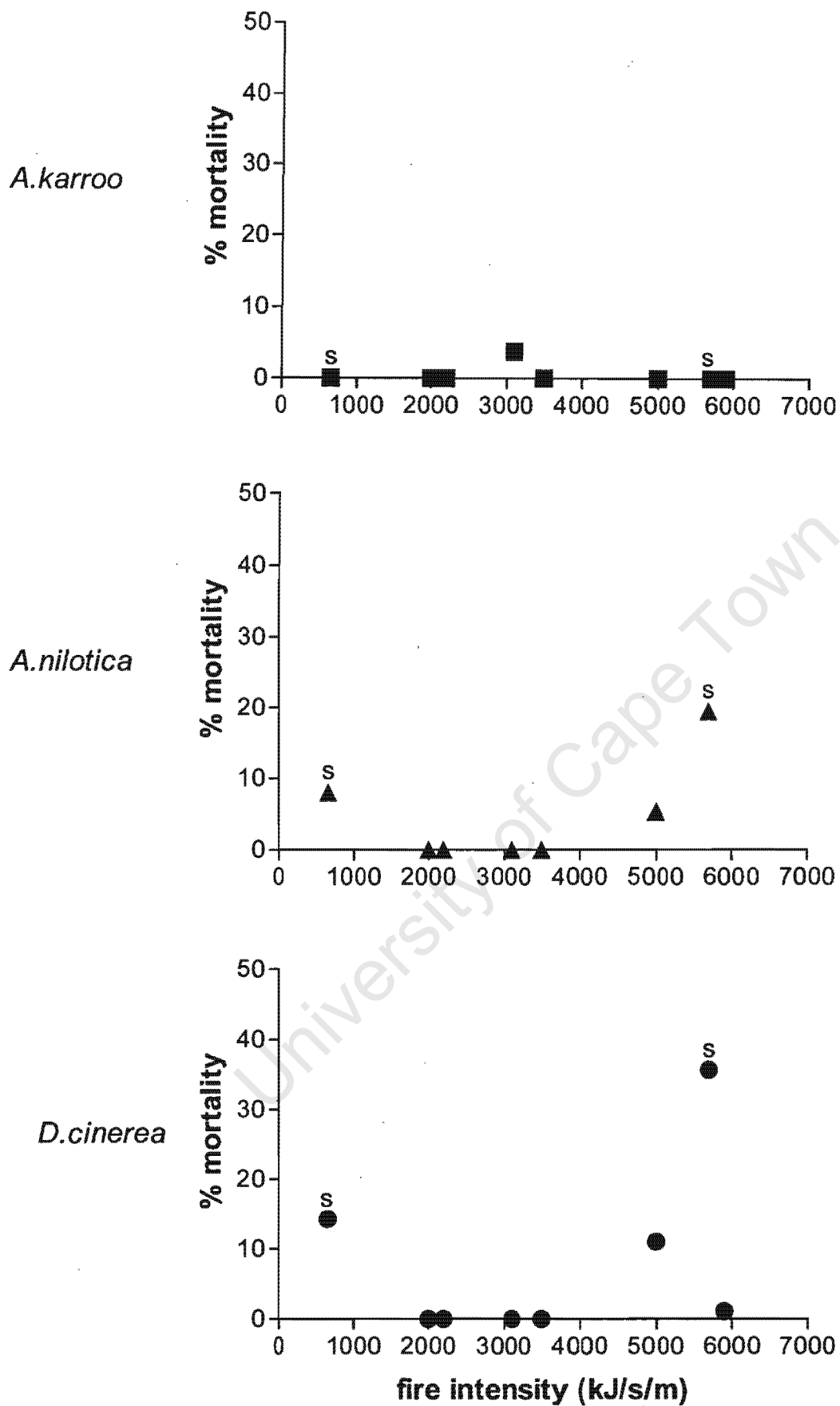


Figure 3.2 Effect of fire intensity on mortality in three tree species found after eight controlled burns in the HUP. S = summer burns.

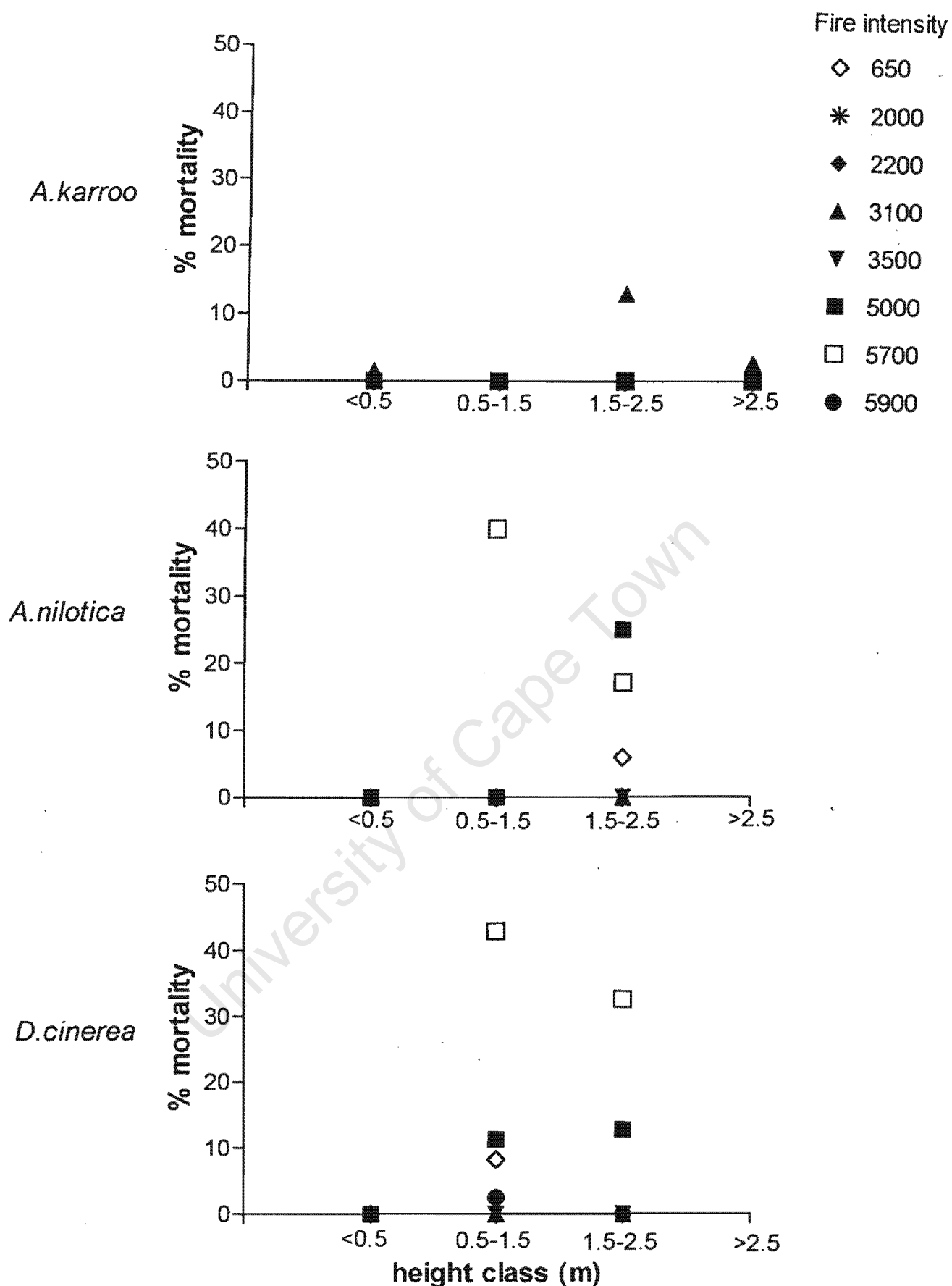


Figure 3.3 Effect of pre-burn tree height on tree mortality in three tree species. Fire intensity of each burn is shown in the legend (kJ/m/s). Markers: winter burns filled, summer burns, not filled.

3.4.2.2 Tree mortality

a) Effects of fire season

Figure 3.1 shows the effect of fire season on tree mortality combined for all height classes in the summer and winter burns. Summer fires had a significant effect on tree mortality in *A.nilotica* and *D.cinerea*. Both *D.cinerea* and *A.nilotica* showed highest mortality in the 0.5-1.5m height class following the intense summer fire (5700 kJ/s/m).

b) Effects of fire intensity

Figure 3.2 and Appendix 3.1 show the total percentage mortality per species for each of the eight controlled burns. With the exception of a low intensity summer fire, the effects of fire intensity, when viewed across all species, showed a clear pattern. Fires at or exceeding 5000kJ/s/m showed greater variation in levels of tree mortality with up to 36% mortality of *D.cinerea*. Fire intensities lower than 4000kJ/s/m showed very low tree mortality. However, significant mortality of *A.nilotica* and *D.cinerea* was observed in a single low intensity summer burn.

In *A.karoo* very little mortality was observed and in most fires recorded mortality levels were zero. The highest level of mortality recorded in *A.karoo* was 13.2% at 3100 kJ/s/m. *A.karoo* had lowest mortality levels of all three study species and variability does not appear to be related to fire intensity. In *D.cinerea* and *A.nilotica* higher levels of mortality at fire intensities of >5000 kJ/s/m were observed. The ranges in mortality observed at >5000kJ/s/m was 0-43% in *D.cinerea* and 0 – 40% in *A.nilotica*.

c) Height dependent mortality

Within this general pattern there was further variation within and between species. Figure 3.3 shows the percentage mortality separately for each species with percent mortality shown in relation to pre-burn height class across a range of fire intensities (from Appendix 3.1).

In the <0.5m height class pre-burn stems were mostly totally consumed during the fire. However, it is expected that in all species highest mortality rates would occur in trees in the <0.5m height class. The fact that data is limited for height classes <0.5m and >2.5m was a limitation in the study.

Figure 3.3 shows that there is no clear relationship between mortality and pre-fire height in *A.nilotica* and *D.cinerea*. This was partly due to the limited sample size and range of tree heights present at the study sites for these species. With the exception of the intense summer fire (5700 kJ/s/m) where *D.cinerea* and *A.nilotica* showed highest mortality in the 0.5–1.5m height class, mortality was evident in the 1.5–2.5m height class over a broad range of fire intensities in both species.

3.4.2.3 Topkill rates

a) Effects of fire season

Figure 3.4 shows the effect of fire season on levels of topkill in trees. Data were combined for all height classes in the two summer and six winter burns. Summer and winter fires did not differ in the levels of topkill in *A.karoo* and *D.cinerea*. However in *A.nilotica* summer fires caused approximately 30% lower levels of topkill than winter fires.

b) Effects of fire intensity

Figure 3.5 shows the total percentage topkill for each of the study species following eight controlled burns of different fire intensity. Percentage topkill was highly variable and increased with an increase in fire intensity. Some of the variation was explained by species differences. In *D.cinerea*, percent topkill was almost always 100 %. In *A.karoo* and *A.nilotica* topkill rates were more variable across different fires. *A.karoo* and *A.nilotica* showed a general increase in topkill with increasing fire intensity.

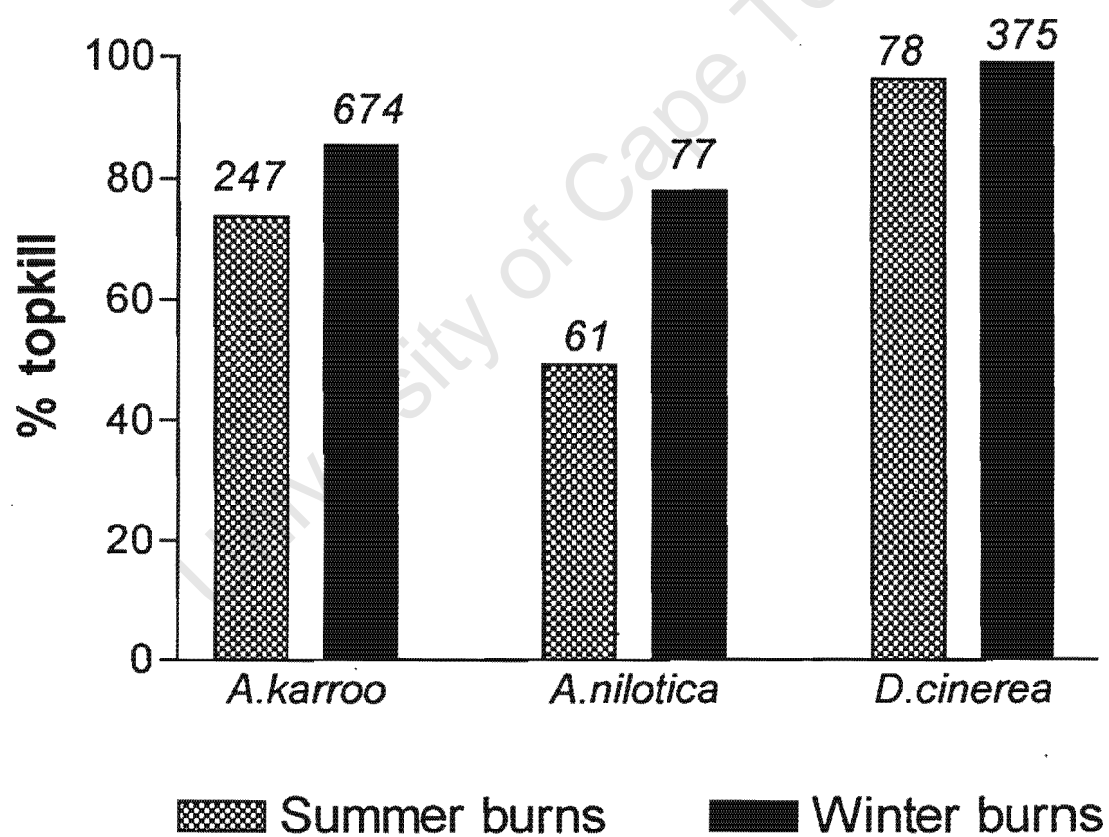


Figure 3.4 Percentage of topkill in trees following two summer burns and six winter burns in the HUP. Number of trees sampled is indicated above the bars.

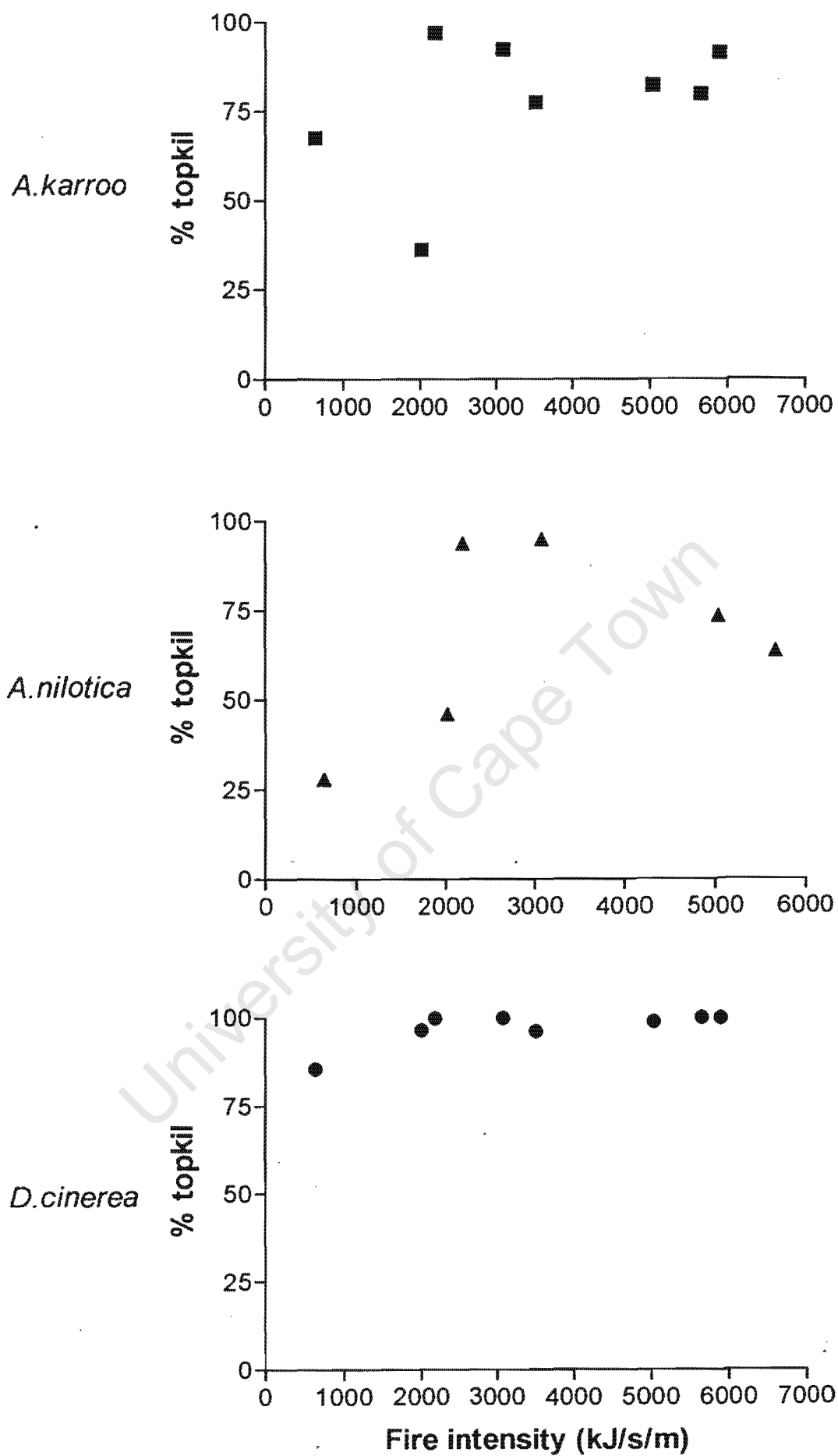


Figure 3.5 Effect of fire intensity on topkill in three tree species found after eight controlled burns in the HUP.

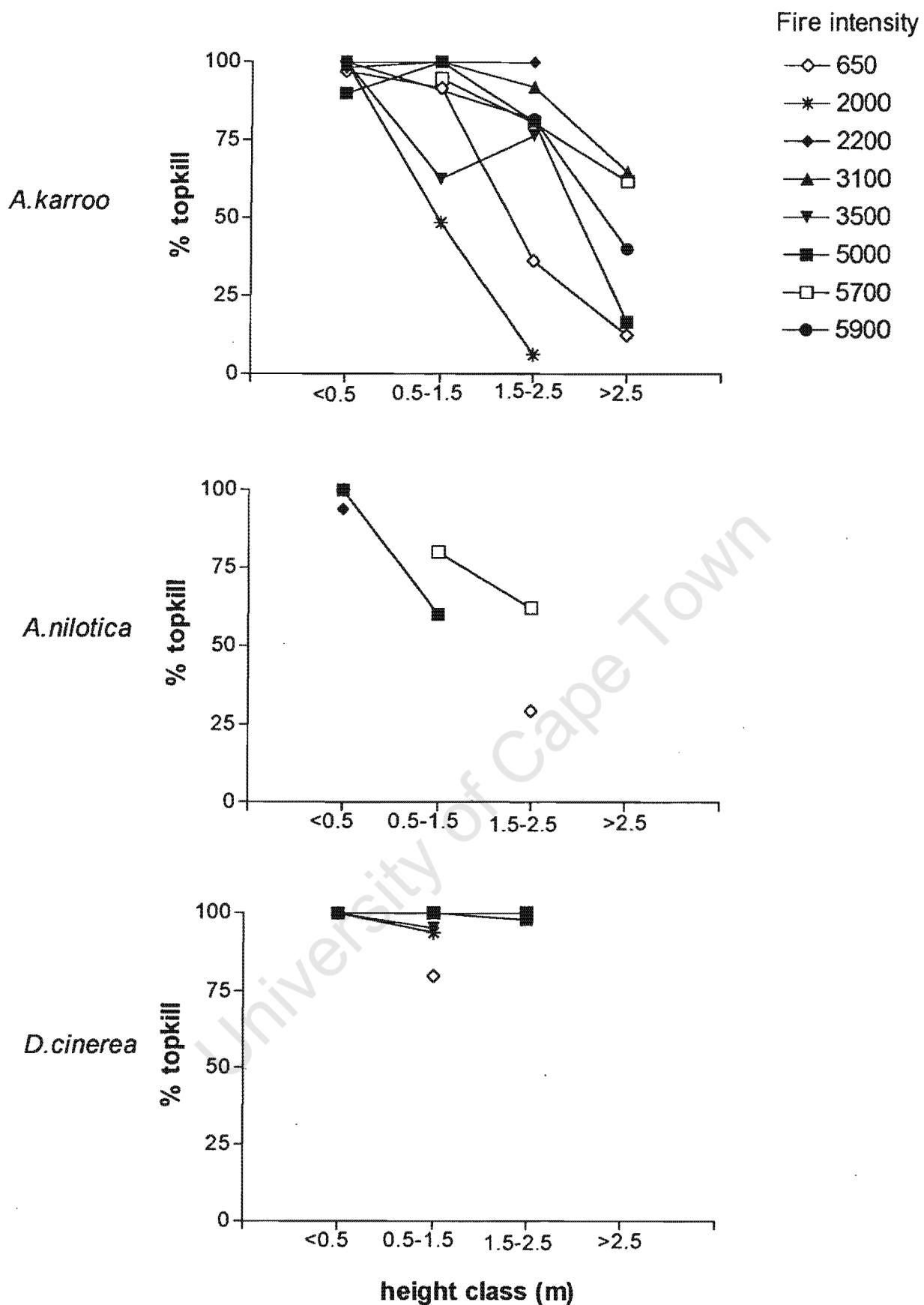


Figure 3.6 Effect of pre-fire tree height on topkill for each tree species found in eight controlled burns in HUP. Fire intensity of each burn is shown in the legend (kJ/m/s).

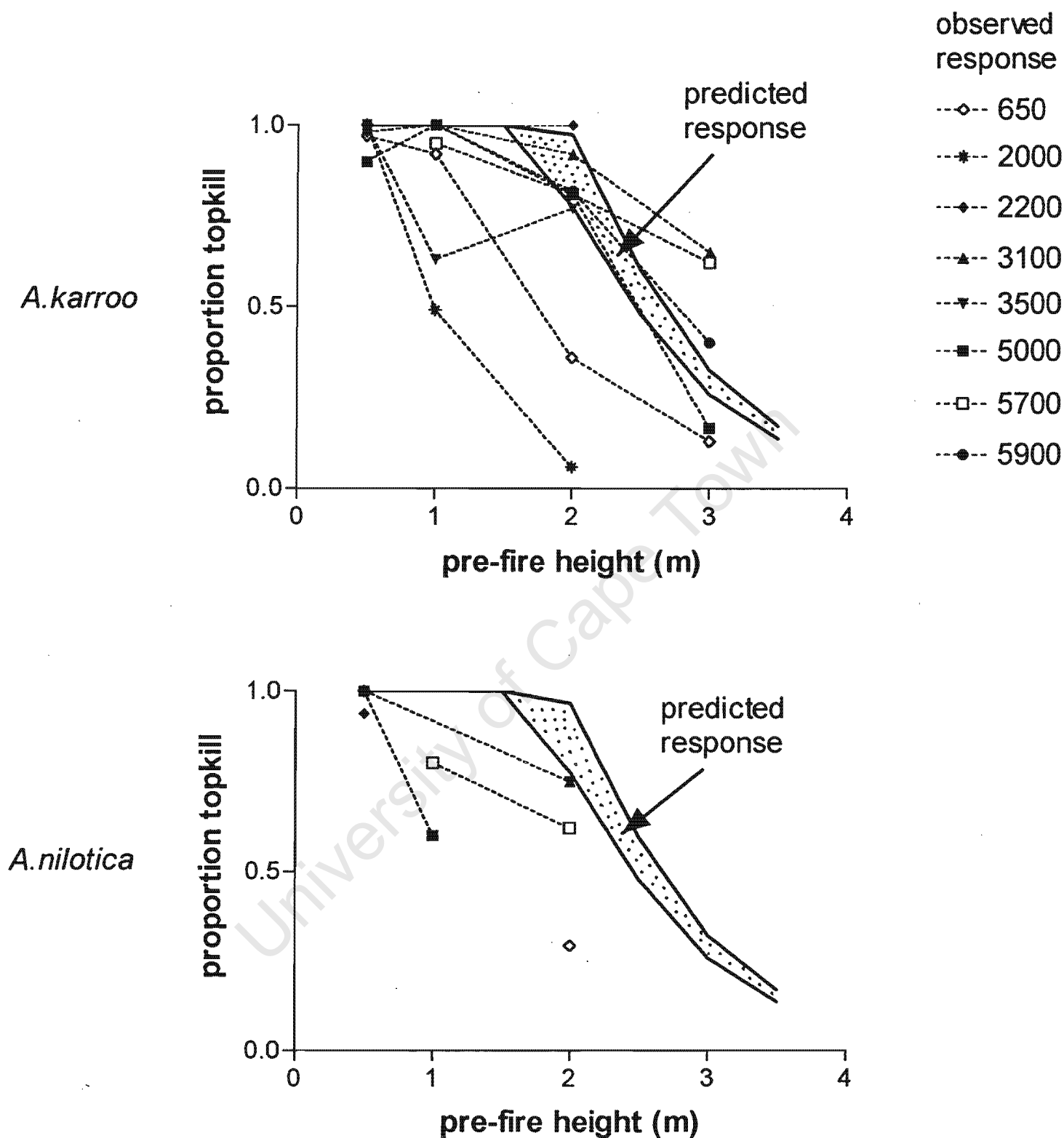


Figure 3.7 Probability of topkill in relation to tree height as predicted by Higgins *et al.* (2000) (hatched) and compared with observed topkill levels in this study. Predicted topkill is shown for the range of observed fire intensities (650-5900kJ/m/s).

c) Effect of tree height on levels of topkill

Figure 3.6 shows the percentage topkill in each species in each height class for each controlled burn (from Appendix 3.1). In *A.karoo* levels of topkill clearly decreased with increasing pre-fire tree height in most of the burns, and within each height class, variation appeared to be related to fire intensity. In *A.nilotica* levels of topkill also appeared to be related to pre-fire height. A combination of fire intensity and height appeared to explain the variation observed. Topkill was not related to tree height in *D.cinerea*.

d) Predicted versus observed levels of topkill

Figure 3.7 shows the expected rates of topkill predicted by the Higgins *et al.* (2000) model, and the observed rates of topkill for controlled burns. The model approximated tree response in *A.karoo* in burns greater than approximately 3000kJ/m/s but overestimated the proportion topkill at lower fire intensities. In *A.nilotica* the model overestimated topkill.

3.4.2.4 Regrowth rates

In topkilled trees, regrowth vigour was compared across the eight controlled burns. Species showed differences in terms of regrowth vigour and this varied with fire season and intensity as well as pre-fire tree height.

a) Effect of fire season

The effect of fire season on regrowth vigour could not be adequately assessed due to the time differences between winter and summer burns, and regrowth measurements. Summer burns were not included in most of the regrowth analysis since measurements were taken six months post fire whereas winter fire were measured 11 months post fire. At 18 months post fire, most of the pre-fire stems had been knocked over or damaged. It was however possible to compare mean height of regrowth for one summer fire (Zinquimeni, 650 kJ/s/m) at 18 months post fire (Figure 3.8) with the actual regrowth heights in the winter burns.

Figure 3.8 suggests that fire season has little effect on regrowth height in *A.karoo*. However in *A.nilotica* and *D.cinerea*, mean regrowth height after the summer burn is lower than in the winter burns.

b) Effect of fire intensity

When tree regrowth was compared across the six winter burns (Figures 3.9.1-3.9.3) fire intensity did not appear to have any consistent effect on regrowth rates in the three species. To investigate the effect of fire intensity further, an ANOVA of the proportion of regrowth of the pre-fire height, was performed for trees in the 1-2m height class (Figure 3.10). *A.nilotica* was omitted from the analysis due to the small sample sizes (i.e. only trees with persisting pre-fire stems were used in the analysis and in *A.nilotica* a high proportion of trees had lost their pre-fire stems). Homogeneity of variances of proportion regrowth and pre-fire height was tested using Bartlett Chi-square and were not significant in *D.cinerea*, but was significant for the proportion regrowth in *A.karoo* at $p < 0.05$. Therefore a non-parametric test was performed for *A.karoo*.

In *A.karoo* although there was a significant difference in response between different fires, this was not related to fire intensity ($df = 4$ Chi-square = 22.37 $F = 20.22$ p level = 0.0002). In *D.cinerea*, the proportional regrowth was significantly different among fires ($df = 3$ $F = 25.72$ p level = 0.0000), however differences in regrowth were not related to fire intensity.

c) Effect of pre-burn tree height

A.karoo and *D.cinerea* show faster rates of regrowth than *A.nilotica* (Figures 3.9.1-3.9.3). In *A.karoo* and *D.cinerea* most trees that were $< 1\text{m}$ before the burn are able to exceed their pre-burn height within one year. *D.cinerea* had slower regrowth rates than *A.karoo* in trees $> 2\text{m}$ pre-fire height. Trees taller than 2m before the burn showed lower regrowth rates. In *A.karoo* trees $> 2\text{m}$ were also more likely to escape topkill. The smaller sample sizes in *A.nilotica* did not allow for a complete comparison between species.

Linear regressions of proportion regrowth and pre-burn height were used to explore the overall variation in regrowth response between species following winter burns (Figure 3.11). *D.cinerea* and *A.karoo* showed a similar response and the slopes were not significantly

different ($df = 394$, $F = 0.06$, $p \text{ level} < 0.0001$). However differences between the y-intercepts were highly significant ($df = 395$, $F = 18.36$, $p \text{ level} < 0.0001$) and showed that *D.cinerea* was 7% more efficient at regrowth than *A.karoo* following winter burns. The response of *A.nilotica* was very different to the other species, below pre-burn height of approximately 1.3m regrowth rates were higher than in *A.karoo* and *D.cinerea* but rapidly tails off in trees above 1.3m.

Table 3.2 Average height (and standard deviation) of trees that escaped topkill in *A.karoo* and *A.nilotica*. No figures are shown for *D.cinerea* since very few trees escaped topkill. Pre-burn heights of escaped trees fell within the range of topkilled trees (see Figure 3.12). (nd = no data)

SPECIES		SITE NAME							
		Magangeni	Zidonini	Masendwini	Masendwini	Zinquimeni	Zinquimeni	Gontshi	Umfoloji
				R	L	winter	summer		summer
<i>A.karoo</i>	Average height (m)	2.61	1.66	1.43	2.76	1.71	2.12	2.64	2.39
	STD	0.35	0.28	0.41	0.39	0.29	0.51	0.46	0.59
<i>A.nilotica</i>	Average height (m)	1.26	1.4	nd	nd	nd	1.74	nd	2.02
	STD	0.22	0.25				0.33		0.33

d) Height growth of trees that escaped topkill

Linear regressions were used to compare regrowth rates of *A.karoo* and *A.nilotica* trees that escaped topkill and those that were topkilled (Figure 3.12). No data is shown for *D.cinerea* since very few trees escaped topkill. Trees that escaped topkill sprouted epicormically (i.e. on the stem) from areas of the stems that were not killed during the burn. In *A.karoo* many trees that escaped topkill had not reached their pre-burn height within a year after burning. In *A.karoo* the slopes of topkilled and escaped trees were significantly different ($df=236$, $F = 14.04$, $p \text{ level} = 0.0002$). In *A.nilotica* the slopes of topkilled and escaped trees were similar to those of *A.karoo*.

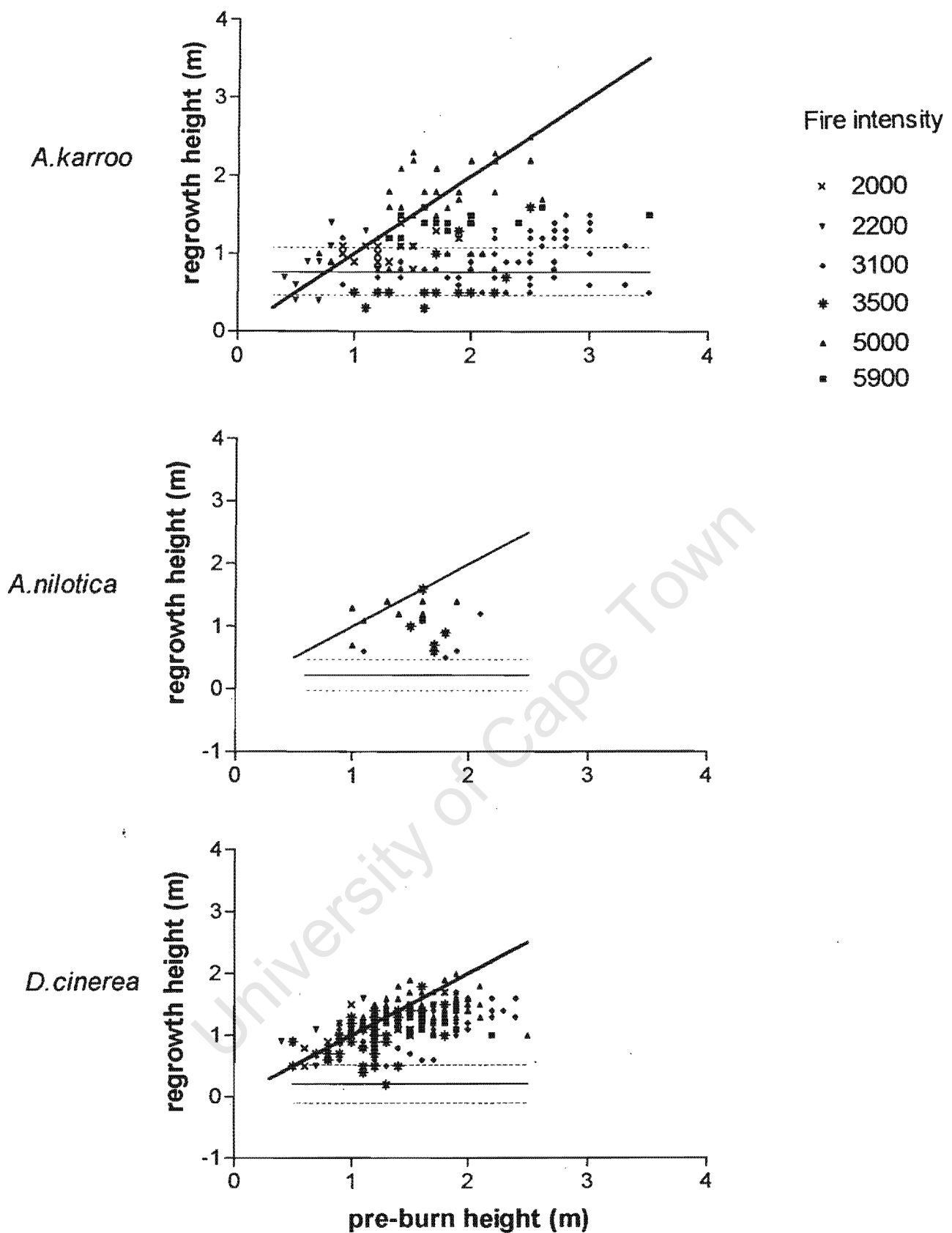


Figure 3.8 Relationship between pre-burn and regrowth height in the three study species compared for summer and winter burns (legend = fire intensity in $\text{kJ/m}^2/\text{s}$). Regrowth measurements at 18 months post fire were only available for one summer burn. The diagonal indicates regrowth equal to that of the pre-burn height. The solid horizontal line represents the mean regrowth height of trees following a summer burn and the dashed lines the standard deviation.

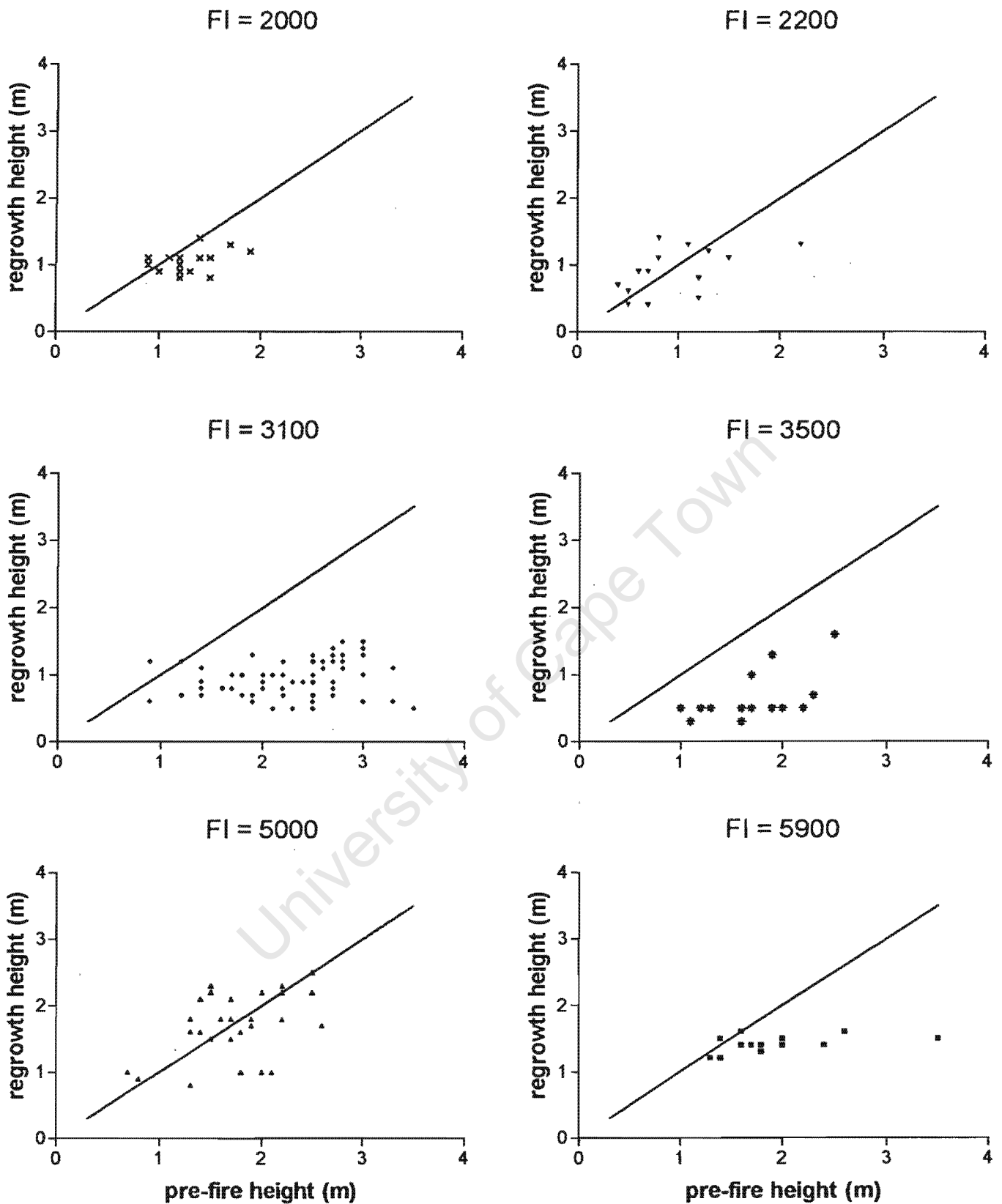
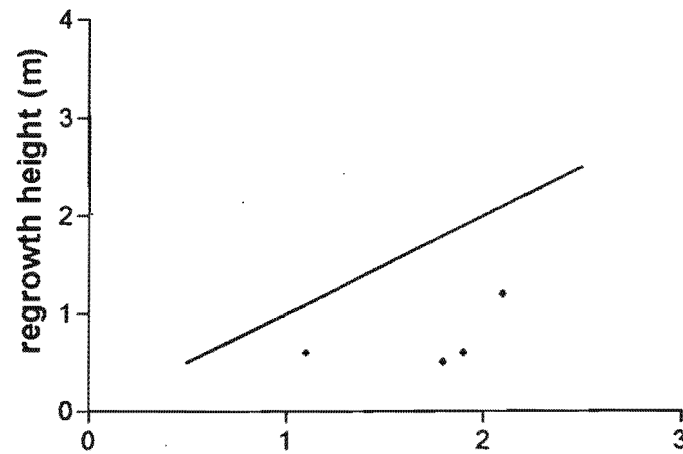


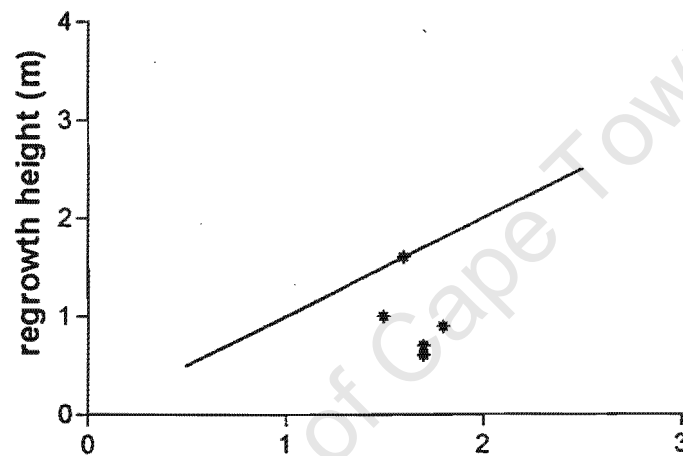
Figure 3.9.1 Relationship between pre-burn and regrowth height in the three study species shown separately for each of the winter burns in *A.karoo*. The diagonal indicates regrowth equal to that of pre-burn height. FI = fire intensity in kJ/m/s.

FI = 3100

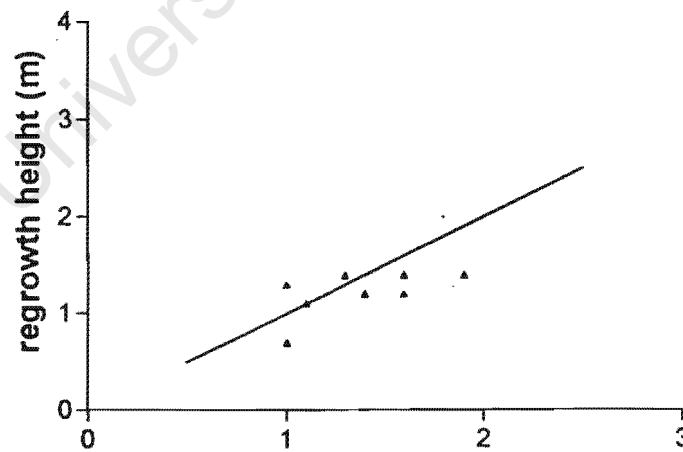
A. nilotica



FI = 3500



FI = 5000



pre-fire height (m)

Figure 3.9.2 Relationship between pre-burn and regrowth height in the three study species shown separately for each of the winter burns in *A. nilotica*. The diagonal indicates regrowth equal to that of pre-burn height. FI = fire intensity in kJ/m/s.

D.cinerea

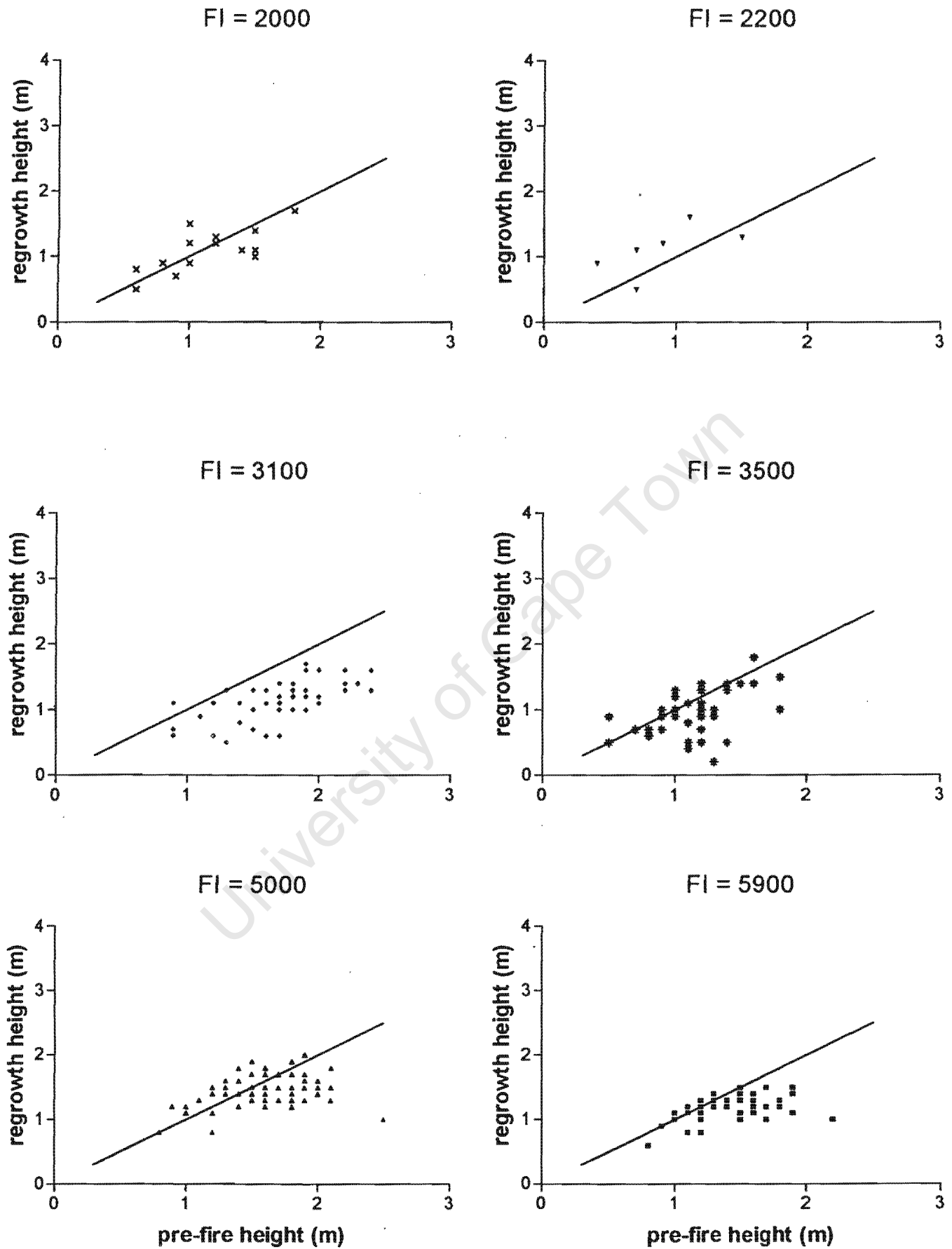


Figure 3.9.3 Relationship between pre-burn and regrowth height in the three study species shown separately for each of the winter burns in *D.cinerea*. The diagonal indicates regrowth equal to that of pre-burn height. FI = fire intensity in kJ/m/s.

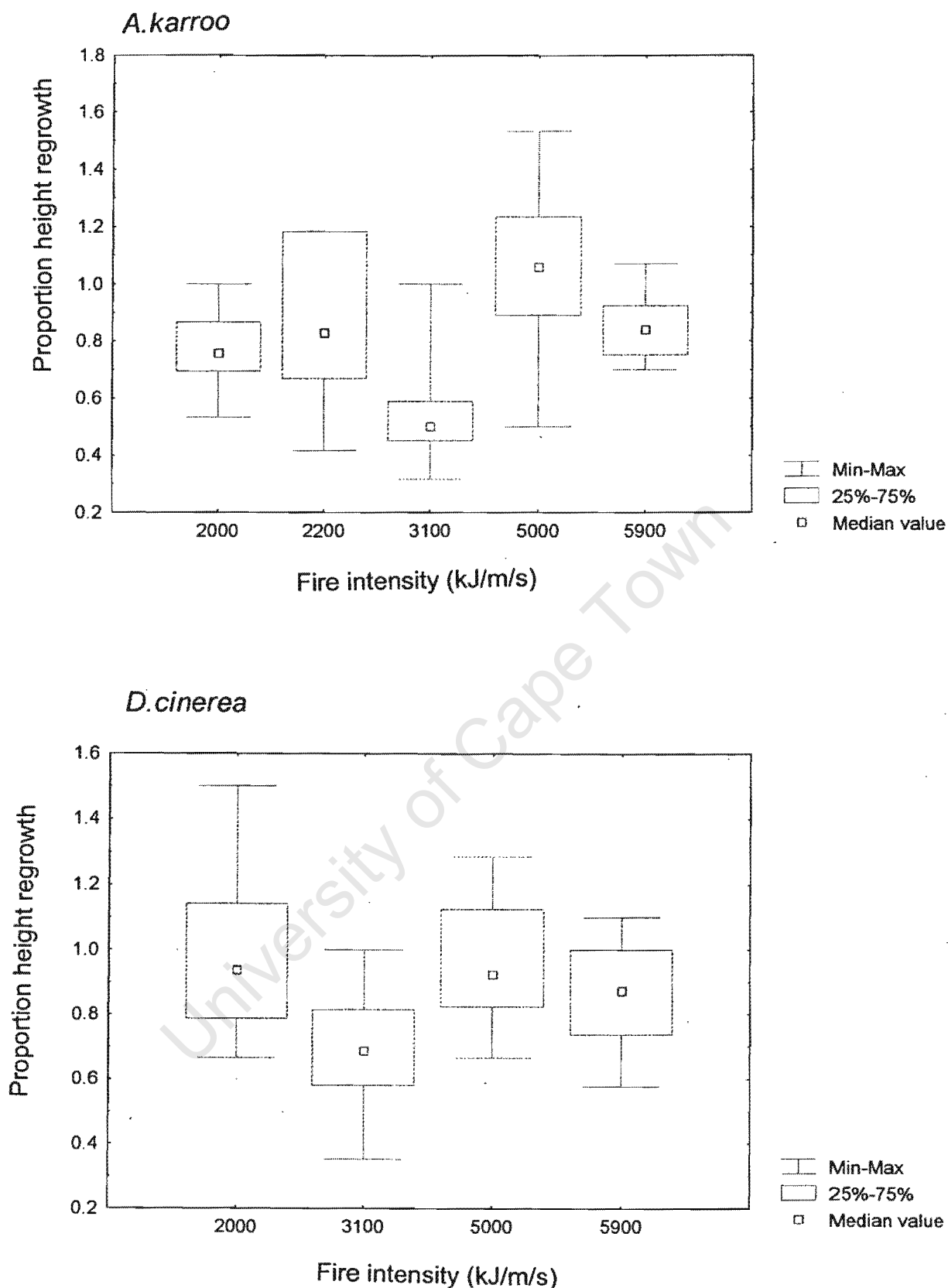


Figure 3.10 Categorized box whisker plot of proportion of height regrowth (height 1 yr post-burn/pre-burn height) versus fire intensity for the six winter burns in *A.karoo* and *D.cinerea*. Only trees in the 1-2m pre-fire height class were used. See text for results of statistical tests of variance.

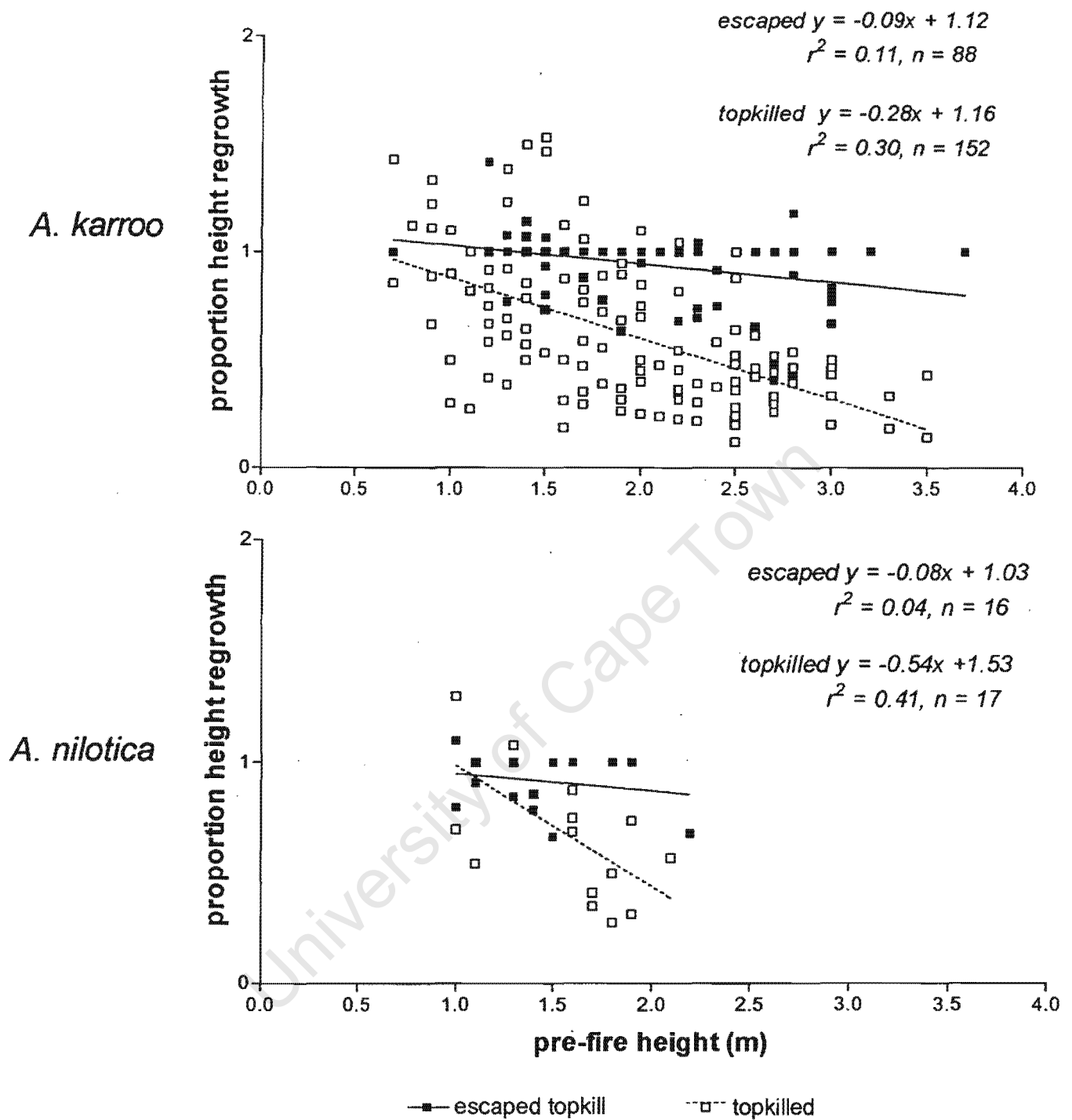


Figure 3.11 Linear regressions of proportion of height regrowth versus pre-burn tree height combined for the six winter burns in three study species. The regression equations, sample size (n) and r^2 are shown on the graph (significance levels: *A.karroo* ($p < 0.0001$), *A.nilotica* ($p = 0.004$) and *D.cinerea* ($p < 0.0001$)).

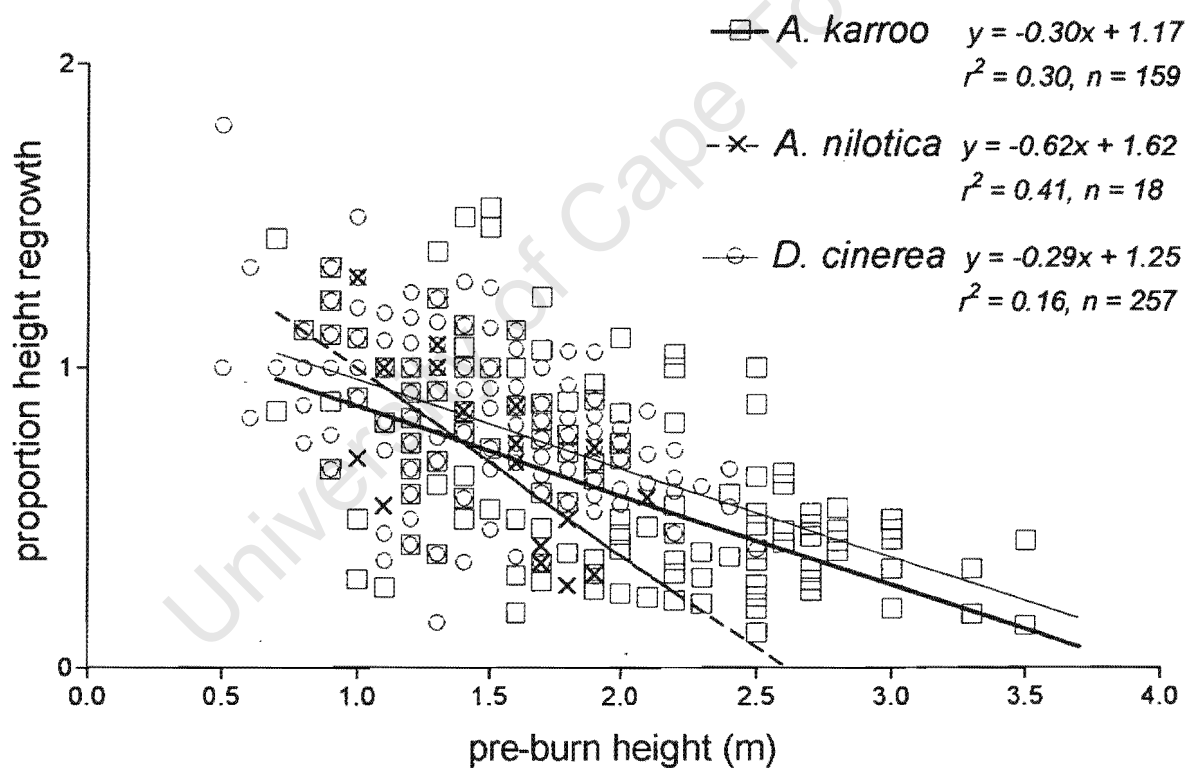


Figure 3.12 Comparison of height growth in *A.karroo* and *A.nilotica* trees that were topkilled with trees that escaped topkill (i.e. these trees were scorched but not topkilled) relative to pre-burn tree height. Data were combined for all six winter burns. The regression equations, sample size (n) and r^2 are shown on the graphs ((significance levels: *A.karroo* topkilled ($p < 0.0001$), *A.karroo* escaped ($p < 0.002$); *A.nilotica* topkilled ($p = 0.006$) *A.nilotica* escaped (not significant)).

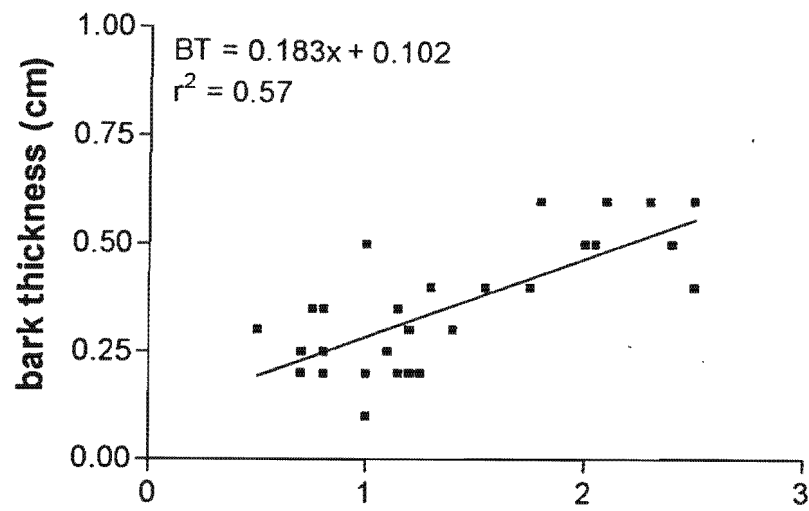
3.4.3 Bark thickness

A.nilotica has the thickest bark of the three species. Figure 3.13 shows the relationship between bark thickness and tree height for the three study species. Bark thickness predicted by the regression equations displayed on Figure 3.13, is shown across a range of tree heights in Table 3.3. Bark thickness at different heights can be compared with the average height of trees that escape topkill (Table 3.2). In *D.cinerea* all trees <2.5m are topkilled. This may be due to the thinner bark of this species. However, in *A.karoo*, which has similar bark thickness, this does not hold. Thus bark thickness does not explain the lower levels of topkill observed in *A.karoo*. However, in *A.nilotica* bark thickness may explain the lower levels of topkill observed as well as the lower height of trees that escape topkill.

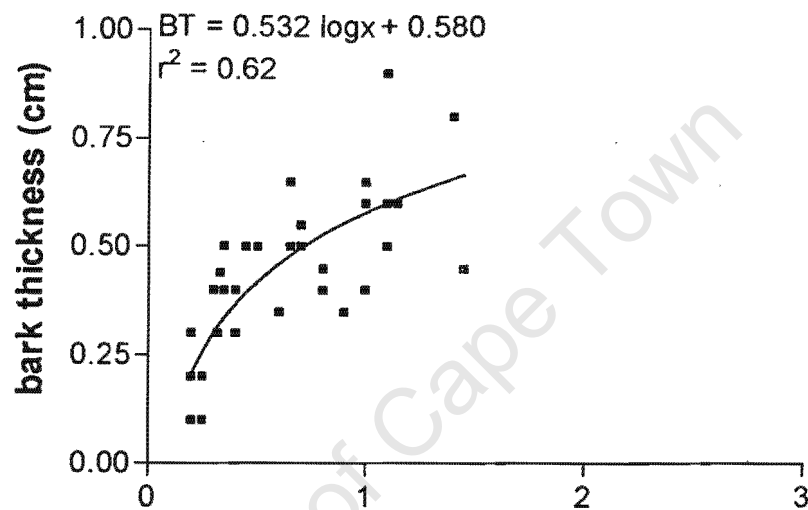
Table 3.3 Bark thickness (cm) at different tree heights predicted by the regression equations in Figure 3.13.

Species	Tree height (m)				
	0.5	1	1.5	2	2.5
<i>A.karoo</i>	0.2	0.3	0.4	0.5	0.6
<i>A.nilotica</i>	0.4	0.6	0.7	0.7	0.8
<i>D.cinerea</i>	0.2	0.2	0.3	0.3	0.4

A. karroo



A. nilotica



D. cinerea

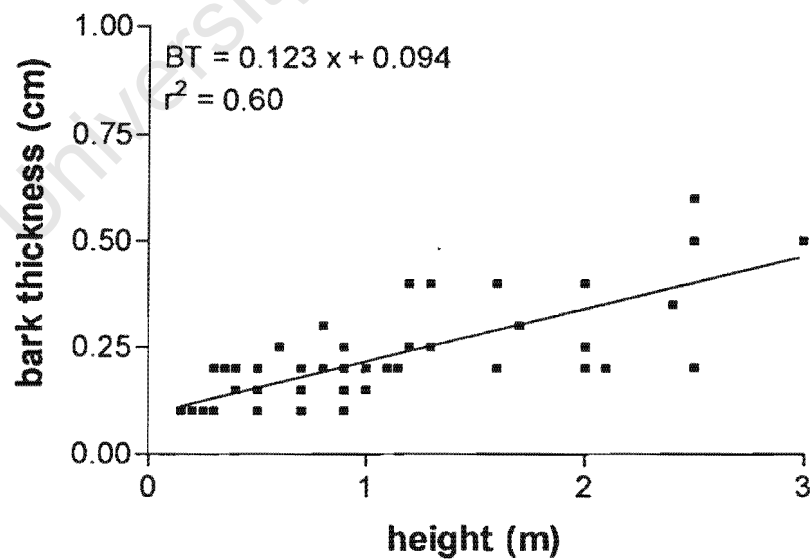


Figure 3.13 Relationship between bark thickness and tree height for the three study species. Regression equations, sample size (n) and r^2 are shown on each graph. (all significant at $p < 0.0001$).

3.5 Discussion

3.5.1 Fire intensity measurements

The range of fire intensities estimated for the eight controlled burns fell within the range found by van Wilgen and Wills (1988) (194-5993 kJ/s/m in ten experimental burns in northern Natal). Most fires in this study fell in the "extremely hot" category according to Trollope (1998). Van Wilgen and Wills (1988) found mean fuel load to be 3800kg/ha which is at the lowest end of the fuel load range found in this study. This suggests that the Eastern Cape calibration of the disc pasture meter used in this study may have produced overestimates of fuel loads in HUP. In turn this would have affected the overall estimates of fire intensity.

3.5.2 Tree response

3.5.2.1 Species abundances

Do the survival strategies and patterns of survival/mortality explain species abundances in the HUP? The low rates of mortality and high regrowth rates following topkill by fires of varying intensity and season may explain the abundance of *A.karoo* relative to the other two species. This is consistent with Bond *et al.*'s (in press) hypothesis that greater fire tolerance of this species accounts for its dominance in tall grass areas in the HUP.

3.5.2.2 Patterns of mortality

There was a high degree of variation in levels of mortality between the three species in the study. Fire season, fire intensity and pre-fire tree height accounted for much of the variation observed. *A.karoo* showed negligible mortality rates in all fires studied. However, fire intensity is expected to affect mortality significantly in <0.5m height trees in the three study species given the mortality figure obtained in the clipping experiment (Chapter 2). *D.cinerea* and *A.nilotica* had higher overall tree mortalities than *A.karoo*, mostly at fire intensities >5000kJ/s/m. In both species mortality was significantly higher for the summer season burns suggesting that physiologically they are more susceptible to wet season fires than dry

season fires. The underlying mechanism for this is explored further in the following chapter. The data for *D.cinerea* and *A.nilotica* also suggest that the risk of tree mortality increases with tree height.

The limited sample size for height classes <0.5m and >2.5m was a weakness in the study. This problem could be overcome for the <0.5m class by marking each individual before the fire. However, this is not a trivial exercise given the logistics and cost involved in finding and marking seedlings, as well as the risk that a controlled burn may not take place. The lack of sufficient numbers of >2.5m trees in *A.nilotica* and *D.cinerea* in the eight burns was also a limitation, but here results from the clipping experiment provide a good indication of tree response.

For height classes 0.5-1.5m and 1.5-2.5m comparison with results from the clipping experiment for mortality and regrowth rates (Chapter 2) showed that in *A.karoo* mortality levels were similar after both clipping and fire treatment. Due to the smaller sample sizes in *A.nilotica* for the 0.5-1.5m height class this comparison was not possible. In *D.cinerea*, mortality levels found in the clipping study were lower than found in several of the controlled burns. This suggests that fire might damage the bud tissue in the root crown.

Response of tree seedlings to fire could not be tested here. However, one can speculate about the possible differences between clipping and fire. Although research on soil heat profiles (Bradstock and Auld 1995) shows that the soil acts as a good insulator, protecting the root crown from excessive heat, Hodgkinson (1998) found that fire caused greater mortality than clipping.

Mortality is perhaps an inappropriate variable for dealing with issues of bush management since in general, fire induced mortality in savannas trees is low (Trollope 1974 and Hopkins 1965 found 7-8% mortality; Lonsdale and Braithwaite 1991 found 14.3% mortality).

3.5.2.3 Patterns of topkill

Species showed variation in levels of topkill depending largely on fire intensity and pre-fire tree height. Fire season did not affect levels of topkill significantly in *A.karoo* and *D.cinerea*, but caused a 30% reduction in levels of topkill in *A.nilotica*. This result is

surprising, since lower levels of topkill were expected in all species in the summer burns due to higher tree moisture as well as the higher fuel moisture during the wet season (Photo 11-12).

In *A.karoo* and *A.nilotica* variation in topkill rates was explained by a combination of both pre-fire height and fire intensity. However this relationship was less clear in *A.nilotica*. In *D.cinerea* topkill levels were high in all burns and there was very little variation between burns. Thus for *D.cinerea* topkill was easily achievable in the 0.5-2.5m height range. The lack of >2.5m trees in *A.nilotica* and *D.cinerea* limits the comparison with *A.karoo*.

What is the "escape height" at which most trees will survive a burn with no topkill? The answer varies with species. Escape height can be predicted from the relationships between topkill, tree height and fire intensity. For *A. karoo*, trees >1.5m have some chance of avoiding topkill in low intensity burns (< 3000kJ/s/m) while, for high intensity burns, trees need to be above 2.5 m. Field measurements of trees that escaped topkill support these predicted values (Table 3.2) with average tree heights of 2.4 – 2.6m for trees surviving high intensity burns (> 5000kJ/m/s).

In *A.nilotica* levels of topkill were lowest of the three study species, though inferred patterns were based on a small sample size. Field measurements of trees that escaped topkill (Table 3.2) showed that *A.nilotica* trees escaped topkill at lower heights than in *A.karoo*.

For the range of heights studied (i.e. those most common in the HUP), *D.cinerea* trees rarely escaped topkill, except for some trees in a low intensity winter burn.

Can topkill be predicted by fire intensity models? I tested models of Higgins *et al.* (2000) which predicts the frequency of escape from gullivers to mature trees, by simulating how fire intensity and tree size influence the likelihood of topkill. In *A.karoo* (Figure 3.7) the observed levels of topkill closely approximated the predicted values for fire intensities >5000kJ/s/m. However at lower fire intensities there was greater discrepancy between the predicted and observed values.

The lack of data for taller height classes in *A.nilotica* and *D.cinerea* limited the comparison with the model. From the available data, the model generally overestimated levels of topkill

in *A.nilotica*. No figure is shown for *D.cinerea* since almost 100% topkill was observed, and this fits with the predicted levels of topkill. Higgins *et al.* (2000) do not consider species differences, however this study demonstrates that species differences are significant and should be explicitly considered in such models.

3.5.2.4 Regrowth rates

Regrowth of topkilled trees differed within and among species. It appears that pre-fire tree height played a role in this. Fire season may also play a role in affecting regrowth, however, regrowth appeared to be independent of fire intensity. From Figure 3.8 it appeared that *D.cinerea* and *A.nilotica* were negatively affected by wet season burns. *A.karoo* appears unaffected by season of burn. This could be related to carbohydrate storage patterns and will be investigated in more detail in the following chapter.

Fire intensity did not appear to have an effect on tree regrowth height in *A.karoo* and *D.cinerea*. However regrowth height was negatively correlated with pre-fire tree height in these two species. Taller *D.cinerea* plants (> 1.5 m) always reverted to lower height classes, a pattern which may be of use in management of this species.

The linear regressions (Figure 3.11) provided a useful means for comparing the regrowth rates of the three species. Overall *D.cinerea* was 7% more efficient than *A.karoo* in terms of regaining and exceeding pre-burn height. Although data for *A.nilotica* were limited, the regrowth response in *A.nilotica* appeared to be different, with regrowth vigour tailing off relatively rapidly with increasing pre-burn height.

When these regrowth rates were compared with one-year regrowth results from the clipping study (Chapter 2); some interesting differences were observed. *D.cinerea* and *A.karoo* showed similar differences between the results of clipping and controlled burn studies. In *A.karoo* maximum regrowth rates occurred in trees <1.2m in the clipping study and between 1 and 1.8m in the controlled burns. Regrowth rates also tailed off at lower pre-burn heights in the clipping study (i.e. about 1.5m) relative to the controlled burns (i.e. about 2m) in *A.karoo*. This suggests that there may be different physiological affects of clipping versus burning in *A.karoo*. One possible explanation is that some reserves are withdrawn from topkilled stems prior to resprouting or simply that with more light, nutrients and water

available, growing conditions were better after burning. In *A.nilotica*, a fair comparison of response of clipping and controlled burn studies was not possible due to disjunct height classes between the studies.

Clipping was useful for testing the effects of decapitating the smallest and largest size classes, a treatment which was not possible in the controlled burns. The clipping experiments provided insight into sprouting abilities in these height classes and the location of bud banks. Controlled burns allowed better insights into the effects of a range of fire intensities. For *A.karoo* and *D.cinerea*, the clip and burn results showed clearly that there was reduced regrowth vigour in taller trees following topkill.

The comparison in regrowth of topkilled trees and trees that escaped topkill revealed some interesting patterns in *A.karoo*, in that some topkilled trees showed much higher regrowth rates than trees that were not topkilled (Figure 3.12). However the general trend predicted by the linear regression was as expected, and showed that regrowth in escaped trees was faster than those that were topkilled. Further, the overall response predicted by the linear regression suggests that trees >2m that escaped topkill regain their pre-burn height much faster than those topkilled. It would be worth investigating further, whether low intensity burns are more effective in retarding regrowth in intermediate height stands of *A.karoo*, and vice versa. In *A.nilotica* trees that escaped topkill showed higher regrowth rates than topkilled trees as expected.

3.5.3 Bark thickness

Does bark thickness explain species differences in fire survival and escape height? *A.nilotica* escaped topkill at lower tree heights than *A.karoo*, a difference in fire response consistent with *A.nilotica*'s thicker bark (Photo 5). However thick bark alone does not make this species more resistant to burning. *A.karoo* was generally the more fire-resistant species for trees below topkill height since it suffered no mortality and resprouted more vigorously. The difference in resprouting vigour might reflect carbon allocation costs to bark versus height growth (Gignoux *et al.* 1997). It would be interesting to extend this observation to a wider range of tree species.

3.6 Conclusion

The species in this study showed clear differences in their response to burning. High fire intensities can kill *A.nilotica* and *D.cinerea* but not *A.karoo*. Summer burns, an uncommon burning practice in these reserves, killed substantial numbers of *A.nilotica* and *D.cinerea*, but not *A.karoo*. Mortality was higher after summer burns than in the "normal" winter burns in the dormant growth season.

Burning to maximise topkill and prevent increased woody biomass is the only option for *A.karoo*. The escape height (of decreasing probability of topkill) was ca 2.5m in *A.karoo* but less (only 1.5 m) in *A.nilotica* due to its thicker bark. Regrowth after topkill varied among species with tree height. It may be possible to retard regrowth in *A.nilotica* and *D.cinerea* by burning in summer. *D.cinerea* is always topkilled and burning for topkill is not a particularly effective method for controlling densities of this species, though it will influence biomass.

In summary, I recommend further investigation of occasional summer burns as a management practice where *D.cinerea* and/or *A.nilotica* are the species of concern. The practice of aiming for high intensity burns should be re-considered depending on the average height of gullivers. *A.karoo* growth may be retarded more by low intensity burns than high intensity ones where most plants are in smaller size classes (<1.5m).

These results also indicate that species differences must be taken into account when devising management burns. The biological basis for species differences is of intrinsic interest and will be discussed further in Chapter 5.

3.7 References

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APPENDIX 3.1

Summary of data collected for each species from the controlled burns in August 1996. Data includes sample sizes, number of mortalities and number of topkilled individuals. Data was recorded one year after the winter burns and 6 months after the summer burns. In the Zinquimeni summer burn, data was collected again 18 months after the burn, but data not shown.

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3.1.1 *Acacia karroo*. Numbers in italics were excluded from analysis because of the small sample size.

SITE NAME, FIRE SEASON & FIRE INTENSITY									
	Pre-fire stem height class	Magangeni Winter 5000	Zidonini Winter 2000	MasendwiniR Winter 2200	Masendwini L Winter 3100	Zinquimeni winter 3500	Zinquimeni summer 650	Gontshi Winter 5900	Umfoloji summer 5700
Total number Trees sampled	no stem	30	11	221	122	6	27	37	
	<0.5m						5		
	0.5-1.5m	10	33	6	11	8	36	3	19
	1.5-2.5m	21	36	5	38	17	44	11	87
	>2.5m	6			37		8	5	21
	Total	67	80	232	208	31	120	56	127
Number trees topkilled (% of total sample)	no stem	27 (90)	11 (100)	217 (98.2)	122 (100)	6 (100)	26 (96.3)	37 (100)	
	<0.5m						5 (100)		
	0.5-1.5m	10 (100)	16 (48.5)	6 (100)	11 (100)	5 (62.5)	33 (91.7)	3 (100)	18 (94.7)
	1.5-2.5m	17 (81)	2 (6.1)	5 (100)	35 (92.1)	13 (76.5)	16 (36.4)	9 (81.8)	70 (80.5)
	>2.5m	1 (16.6)			24 (64.9)		1 (12.5)	2 (40)	13 (61.9)
	Total	55 (82.1)	29(36.3)	225 (97)	192 (92.3)	24 (77.4)	81 (67.5)	51 (91.1)	101 (79.5)
Number trees dead (% of total sample)	no stem	0	0	0	2 (1.6)	0	0	0	
	<0.5m						0		
	0.5-1.5m	0	0	0	0	0	0	0	0
	1.5-2.5m	0	0	0	5 (13.2)	0	0	0	0
	>2.5m	0			1 (2.7)		0	0	0
	Total	0	0	0	8 (3.8)	0	0	0	0

3.1.2 *Acacia nilotica*. Numbers in italics were excluded from analysis because of the small sample size.

SITE NAME, FIRE SEASON & FIRE INTENSITY									
Pre-fire stem height class		Magangeni	Zidonini	MasendwiniR	Masendwini L	Zinquimeni	Zinquimeni	Gontshi	Umfolozi
		Winter	Winter	Winter	Winter	winter	summer	Winter	summer
		5000	2000	2200	3100	3500	650	5900	5700
Total number Trees sampled	no stem	5	6	16	14	2			
	<0.5m								1
	0.5-1.5m	10	4		1	1	7	2	5
	1.5-2.5m	4	3		4	4	17		29
	>2.5m						1		1
	Total	19	13	16	20	7	25	2	36
Number trees topkilled (% of total sample)	no stem	5 (100)	6 (100)	15 (93.8)	14 (100)	2			
	<0.5m								1
	0.5-1.5m	6 (60)	0		1		1 (14.3)	1	4 (80)
	1.5-2.5m	4 (100)	0		3 (75)	3 (75)	5 (29.4)		18 (62.1)
	>2.5m								
	Total	14 (73.7)	6 (46.2)	15 (93.8)	19 (95)	5 (71.4)	7 (28)	1	23 (63.9)
Number trees dead (% of total sample)	no stem	0	0	0	0				
	<0.5m								
	0.5-1.5m	0	0				0		2 (40)
	1.5-2.5m	1 (25)	0		0	0	1 (5.9)		5 (17.2)
	>2.5m								
	Total	1 (5.3)	0	0	0	0	2 (8)	0	7 (19.4)

3.1.3 *Dichrostachys cinerea*. Numbers in italics were excluded from analysis because of the small sample size.

SITE NAME, FIRE SEASON & FIRE INTENSITY									
	Pre-fire stem height class	Magangeni Winter 5000	Zidonini Winter 2000	MasendwiniR Winter 2200	Masendwini L Winter 3100	Zinquimeni winter 3500	Zinquimeni summer 650	Gontshi Winter 5900	Umfolozi summer 5700
Total number trees sampled	no stem	9	13	8	51	7		26	
	<0.5m					2	3		
	0.5-1.5m	35	16	1	17	42	15	40	14
	1.5-2.5m	47	1		33	4	3	23	43
	>2.5m								
	Total	91	30	9	101	55	21	89	57
Number trees topkilled (% of total sample)	no stem	9 (100)	13 (100)	8 (100)	51 (100)	7 (100)		26 (100)	
	<0.5m					2	3 (100)		
	0.5-1.5m	35 (100)	15 (93.8)	1	17 (100)	40 (95.2)	12 (80)	40 (100)	14 (100)
	1.5-2.5m	46 (97.9)	1		33 (100)	4 (100)	3 (100)	23 (100)	43 (100)
	>2.5m								
	Total	90 (98.9)	29 (96.7)	9 (100)	101 (100)	53 (96.4)	18 (85.7)	89 (100)	57 (100)
Number trees dead (% of total sample)	no stem	0	0	0	0	0		0	
	<0.5m						0		
	0.5-1.5m	4 (11.4)	0		0	0	1 (8.3)	1 (2.5)	6 (42.9)
	1.5-2.5m	6 (12.8)			0	0	2 (66.7)	0	14 (32.6)
	>2.5m								
	Total	10 (11)	0	0	0	0	3 (14.3)	1 (1.1)	20 (35.7)



Photo 9 A high intensity controlled burn ($> 4500 \text{ kJ/m/s}$) in the Hluhluwe-Umfolozi Park in August 1995.



Photo 10 Post fire landscape in the Hluhluwe-Umfolozi Park following a patchy controlled burn, August 1995.



Photo 11 Post-fire landscape. This was a high intensity (approx. 5700 kJ/m/s), late summer burn in the Hluhluwe-Umfolozi Park (March 1996). This photo was taken one month after the burn. Note the high levels of scorching in the *A.karroo* skeletons.



Photo 12 Post fire landscape immediately after a controlled burn of moderate intensity (approx. 3500 kJ/m/s) in the Hluhluwe-Umfolozi Park. Note the lower scorch levels in *A.karroo* relative to photo 11 above. The level of topkill was also lower in this fire relative.

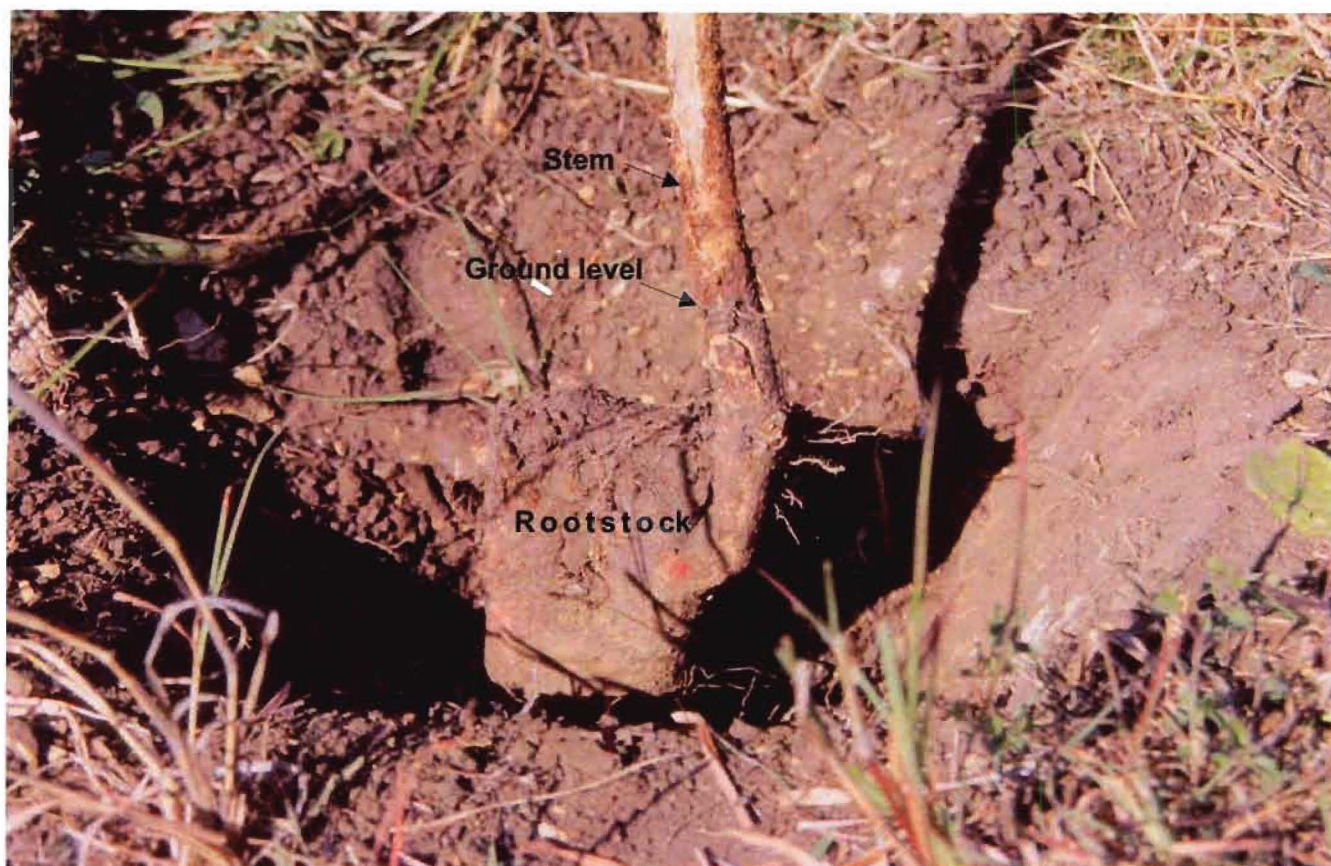


Photo 13 The large rootstock (maximum diameter 15cm) of a 1.5m tall *A.karoo* gulliver.



Photo 14 The narrow lateral root of a 1.5m tall *D.cinerea* tree.

4 TREE RESPONSE TO VARIATION IN SEASON OF DEFOLIATION

4.1 Introduction

Seasonal variation in plant root carbon reserves has been well documented for a variety of species from different systems (Kozlowski 1992). This seasonal fluctuation in carbon reserves has been shown to affect mortality and regrowth potential in several shrub and tree species (Woods *et al.* 1959; Jones and Laude 1960; Bowen and Pate 1993). In some species seasonal fluctuation in carbon reserves closely tracks plant phenology. Many deciduous species exhibit a typical pattern mobilising root reserves when resources are required for spring leaf flush or reproduction. In all resprouting shrubs and trees it is clearly advantageous to have immediate access to a sufficiently large store of readily available energy to maintain what remains of the plant body, and produce a new photosynthetic surface for the shoot recovery process. Starch and other forms of carbohydrate have been shown to be mobilised during the recovery process of certain woody species (Woods *et al.* 1959; Jones and Laude 1960; Kozlowski 1992). Woods *et al.* (1959) found that carbohydrate reserves in the roots of turkey oak (*Quercus laevis*) and bluejack oak (*Quercus incana*) dropped during the spring flush of growth and reached lowest concentrations as the new leaves approached full size (i.e. reserves were half that of dormant periods). In deciduous species, reserves are at their peak just before leaf drop at the end of the growing season. This is currently the favoured burning period in most savannas (Trollope 1984 and 1998).

The quantitative relationships between the amounts of reserves utilised and growth initiated, or, between growth and photosynthesis of new shoots and replenishment of root reserves, have not received much research attention in natural ecosystems (Bowen and Pate 1993).

Bowen and Pate (1993) studied the pattern of starch mobilisation for a Mediterranean shrubland species, *Stirlingia* (Proteaceae). Root starch reserves were depleted by 50-70% of the pre fire storage during the initial few months of shoot recovery after fire. Pre-

fire starch levels were only replenished between 1.5-2 years after a burn. Of significance to this study is that the sequence of shoot regrowth, flowering and establishment of root starch reserves was dependent on the season in which the fire occurred. Plants burnt in summer, following a complete year of vegetative growth, versus plants burnt in spring with just five months of vegetative growth, recovered more rapidly after fire and after two years shoot production was 1.5 times greater than the spring burn (Bowen and Pate 1993). However the fire frequency in this ecosystem is far lower than in mesic savanna systems (i.e. 5-7 yrs).

In African savannas very little attention has been paid to the effects of varying season of defoliation on tree species response (West 1965; Kennan 1971). In South Africa, in particular, the effects of season of burn have been little studied. Exceptions include work on the effects of different season of fire on the grasslands of the KwaZulu Natal Midlands (Everson 1985; Everson and Tainton 1984; Tainton and Mentis 1984) and Thornveld of the Eastern Cape (Trollope 1987). Several grassland studies have shown that fires in summer months are detrimental to the recovery of palatable grasses (e.g. *Themeda triandra*), whereas burning late in the dry season (August – September) while grasses are still dormant was shown to promote them (Everson 1985; Everson and Tainton 1984; Tainton and Mentis 1984). These results from the Natal Midlands have been assumed to apply to grasses in other southern African ecosystems, including savannas. However relatively little is known on the effect of season of burn on grasses in savannas (Hardy *et al.* 1999; Everson 1999).

Few studies have investigated the seasonal effects of defoliation in southern African savanna trees. In the Eastern Cape of South Africa, Teague (1986, 1988a, 1988b) conducted defoliation experiments to test the seasonal effects of browse and shoot production in *A.karoo*. These showed that growth in *A.karoo* is controlled by the environmental factors, and plants could grow opportunistically at any time in the growing season to take advantage of suitable conditions. By growing in flushes and consolidating after each flush, the tree is able to cope with a variable climate and damage by herbivores. Teague and Walker (1988a and 1988b) describe growth patterns of *A.karoo* at different levels of water stress. At least 6 phenological stages were identified in the annual growth cycle, and these along with the pattern of growth were not affected by changes in water stress. Initiation, emergence and development of shoots were

governed by environmental conditions. In field studies on *A.karoo* Teague (1988a) found that it exhibited seasonal fluctuations in total non-structural carbohydrates (TNC) content that is typical of other deciduous species. TNC reserves declined rapidly in spring when the buds started growing. They also declined during rapid leaf, shoot and reproductive organ growth. TNC reserves were replenished while the new leaves were still small. Water stress did not change the pattern of TNC use and replenishment but did slow down the beginning of the next annual growth event as well as the growth of previously initiated organs (Teague 1987). Teague (1988a) suggested that growth flushes followed by replenishment enable *A.karoo* to withstand harsh environmental conditions and browsing damage. *A.karoo* differs markedly from broad-leaved African savanna tree species in its ability to respond to growing conditions in the current rather than in the previous season.

Trapnell (1959) was one of the first savanna ecologists to report on tree response to fires in different seasons. This study, done in northern Zimbabwe on *Brachystegia - Julbernardia* woodland, showed that late dry season burning suppressed woodland development (Trapnell 1959; Chidumayo 1997). Early dry season burning, in contrast, promoted woody growth in miombo woodlands and would be preferred for forest production. Similar patterns of response were found in experiments in Cote d'Ivoire, where after annual burns for 60 years, late dry season burns led to a decrease of the woody component (Louppe *et al.* 1995).

Though marked effects of season of burn have therefore been demonstrated in some African savannas, there is little information for South African species. Nor have analyses been made on the underlying mechanisms of the different seasonal responses as has been done for several taxa in Mediterranean systems. Does seasonal variation in root carbon reserves affect tree/shrub response to injury in savanna?

4.2 Aim of the study

In this chapter I investigate variation in resprouting vigour of three co-occurring deciduous tree species following differing seasons of defoliation by clipping. It is hypothesised that if species exhibit seasonal variation in starch reserves then they should be most susceptible to defoliation or injury when reserves are lowest and vice

versa. This prediction is based on the hypothesis that carbon reserves within the plant vary depending on the phenological cycle of the plant. Whether phenology tracks seasons (i.e. day length and temperature) or rainfall is not clear. Tree sprouting response was compared with root starch reserves and plant phenology.

4.3 Methods

4.3.1 Study area

The study site was located in the western area in the corridor of the Hluhluwe - Umfolozi Park (see Chapter 1 Figure 1.2). For a general description of the Hluhluwe – Umfolozi Park see Chapter 1. Rainfall for the area is approximately 700mm/yr. It was necessary to choose an area within the park that would be fire free until the end of the clipping experiment. The corridor section of the reserve has a history of goat farming before farmers were forcibly removed from this area. Heavy browsing by goats could have placed a significant role in shaping the system seen today. The study area was burnt in August 1993, two years prior to setting up this experiment.

4.3.2 Study species

The three species studied were *A.karoo*, *A.nilotica* and *D.cinerea* which co-occurred in different proportions at the site. *A.karoo* in the 0.7 – 2.5m height range was the dominant woody species in the landscape. Intermediate sized *D.cinerea* trees were also abundant, but *A.nilotica* was scarce. See Appendix B for a full description of study species.

4.3.3 Experimental design

A clipping experiment similar to that described in Chapter 2 was used to explore the effect of season of defoliation on tree response. Four 20 x 30m adjacent plots were staked out along a horizontal slope to enable replication in space and account for any environmental variation. At two monthly intervals for a period of one year (July 1995 – July 1996 inclusive), three randomly selected trees of each species were clipped at ground level in each plot (12 trees in total per treatment). Prior to clipping, their height, number of stems, and

phenological stage was noted. The height class range of trees cut was 0.7 – 2m. Each tree was marked with a metal stake and a numbered tag. At the start of the experiment three trees of each species per plot (12 trees) were measured and marked as controls. The controls remained unclipped for the duration of the experiment and provided normal growth rate and phenology information.

Regrowth of all clipped plants and growth of controls was measured in July 1996 (except those clipped in July 1996). Then on 2nd September 1996 all plots were burnt in a controlled burn. Regrowth of all clipped and control individuals was measured one year later in August 1997 (i.e. after one growing season). Burning all individuals in the experiment provided a useful cut-off point for the experiment for assessing the seasonal effects of defoliation, since time since treatment and the specific growth season can make data analysis complicated. Three measurements of regrowth vigour were made for each tree: height of the tallest stem, total number of stems and sum of the length of all stems. Unfortunately due to very thick and tall regrowth of *Themeda triandra* grass (>1.5m on average) some of the clipped trees could not be relocated during the August regrowth measurements and this reduced the sample size for some treatments.

4.3.4 Data analysis

A 2-way ANCOVA was performed to investigate the response of trees to different season of defoliation with pre-clip height as a covariate (STATISTICA was used for all statistical tests). Controls were not included in any of the ANCOVA's. A 1-way ANCOVA was performed separately for each species with pre-clip height as a covariate to determine the importance of season in explaining tree height response within species. Regrowth height response was regressed against time since clip to determine whether time since clip was important in explaining observed response. Regrowth height response was also regressed against pre-clip height to determine whether pre-clip height influenced regrowth height. 1-way ANOVA's were performed for each species to determine whether there were any differences between seasons in the number of stems produced and the sum of the length of all stems. In all analyses, homogeneity of variances was tested using Bartlett and Cochran's tests.

4.3.5 Root carbohydrate reserves

At each two monthly clipping event, root samples were collected from five individuals of each species adjacent to the four experimental plots (Photo 13 and 14). The height, stem diameter and number of stems of each individual were recorded. Root material was dried immediately at 70°C and stored in silica gel during transport back to the lab. The dried root material was ground to a fine powder and analysed for starch and sugar content using the colorimetric method developed by Buysse and Merckx (1993). This method provides a relatively easy and inexpensive method for analysing total soluble sugar and starch content in plant tissues.

4.4 Results

4.4.1 Regrowth variables

Preliminary ANCOVA's and ANOVA's were performed on all species together and showed significant differences between tree species responses as well as strong seasonal influences. This prompted further investigation of variances within each species.

4.4.1.1 Regrowth height

Figure 4.1 shows the mean pre-clip and regrowth height (measured in 1997) of the three study species clipped at different times throughout the year. Pre-clip height was weakly correlated with regrowth height in *D.cinerea* (Figure 4.2). In all three study species, time since clip was not important in explaining tree response (Figure 4.3). In all three species, pre-clip and regrowth heights were normally distributed and variances were homogeneous ($p < 0.05$).

Although there was little variation in pre-clip height between individuals, it was necessary to further determine the contribution of pre-clip height in explaining the variance. The contribution of pre-clip height was analysed as a covariate in the 2-way ANCOVA

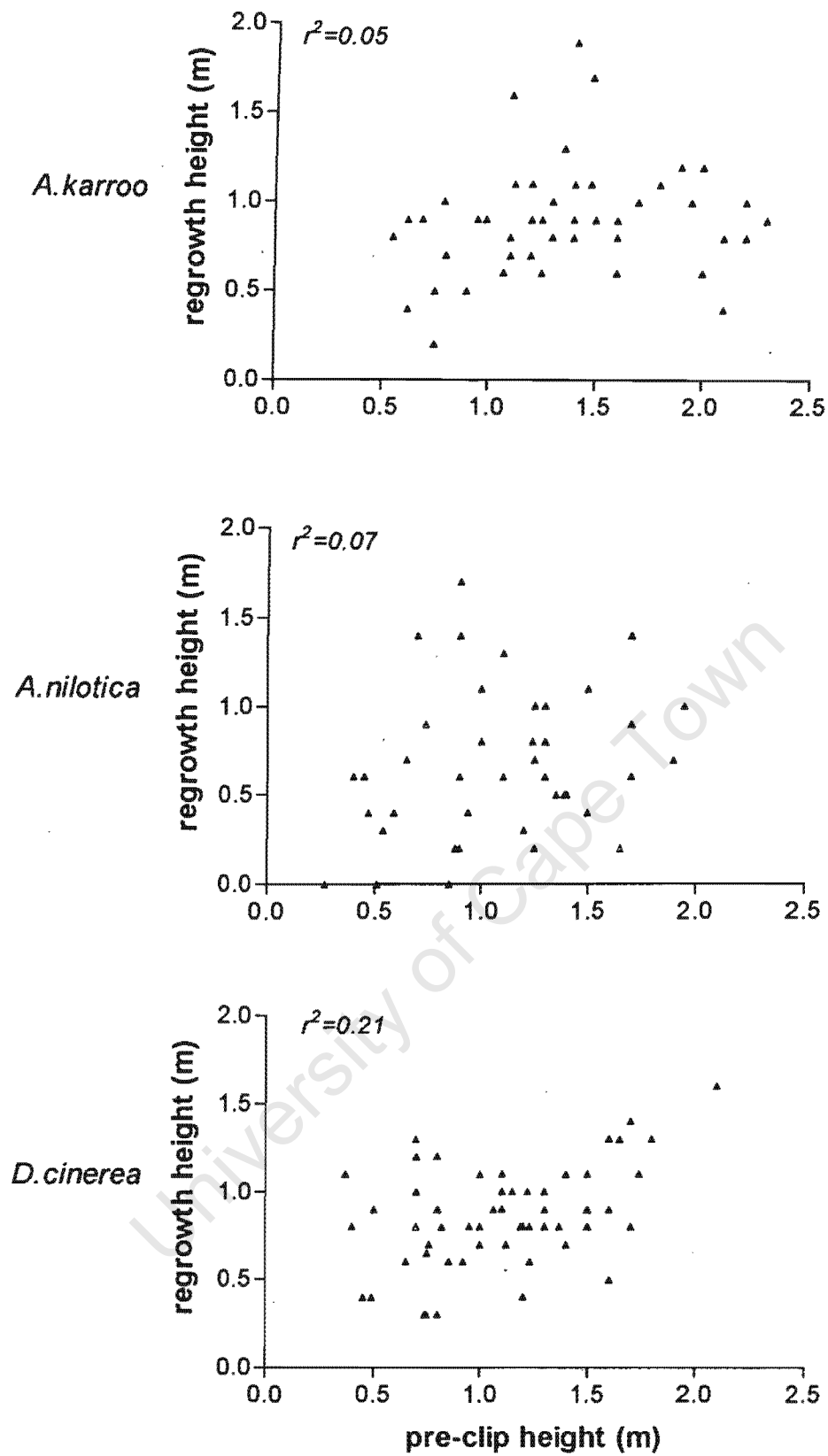


Figure 4.2 Correlation between regrowth height (recorded in August 1997) and pre-clip height for the three study species (*A.karroo* $n = 47$, *A.nilotica* $n = 42$, *D.cinerea* $n = 59$).

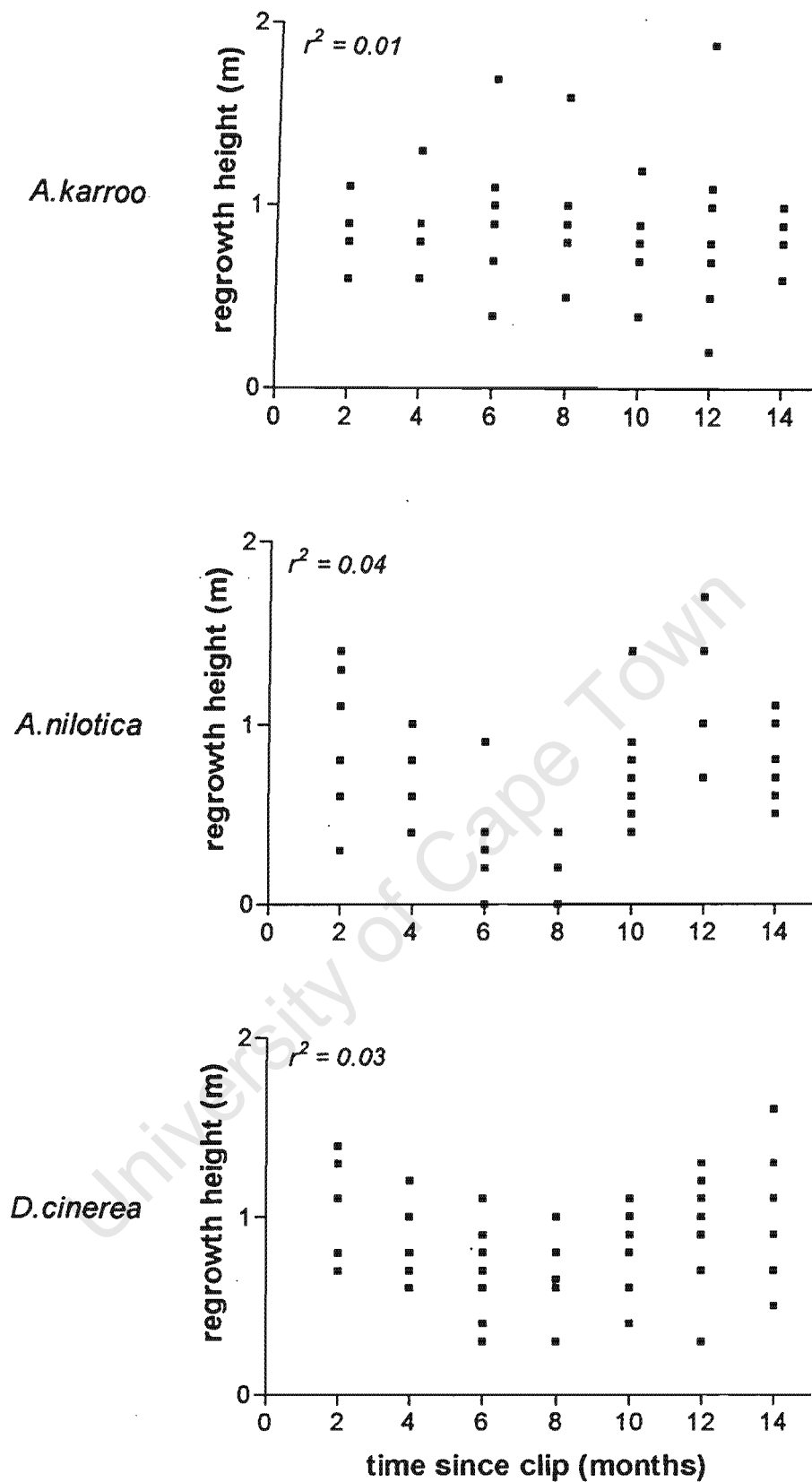


Figure 4.3 Correlation between regrowth height (recorded in August 1997) and time since clip for the three study species (*A.karoo* $n = 47$, *A.nilotica* $n = 42$, *D.cinerea* $n = 59$).

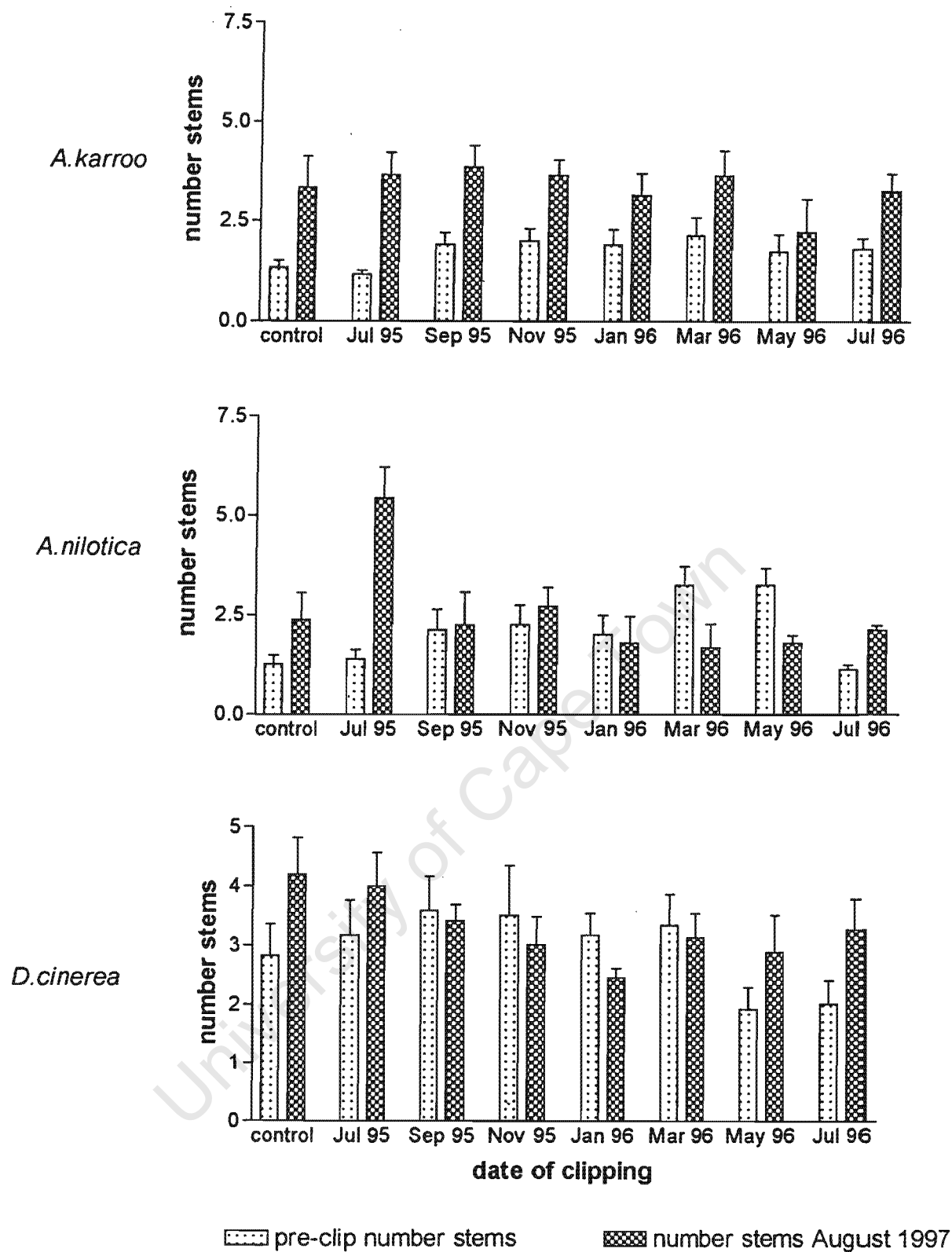


Figure 4.4 Number of pre-clip and resprouting stems (recorded in August 1997) in trees clipped at different times of the year between July 1995 and July 1996. Growth of controls is also shown. Data are means and standard deviations.

(Figure 4.1 and Table 4.1) and was found to be significant. Results from the 2-way ANCOVA show season of clip has a significant effect on tree regrowth while the significant interaction effect indicates that the response varies with species.

Table 4.1 F ratios and significance levels from the 2-way ANCOVA, fixed effects, of species, season of clip and regrowth height. Statistically significant results are shown in bold. Pre-clip height is the covariate.

Effect	df	F	p-level
species	2	3.37	0.376
season	6	4.59	0.0003
interaction	12	2.92	0.0013
Covariate (pre-clip height)	1	15.10	0.0002

Table 4.2 F ratios and significance levels from the 1-way ANCOVA's of tree regrowth height and season of clip. Pre-clip height is the covariate. Statistically significant results are shown in bold.

Effect	df	Regrowth height		df	Covariate (pre-clip height)	
		F	p-level		F	p-level
<i>A.karoo</i>	6	0.89	0.514	1	6.58	0.014
<i>A.nilotica</i>	6	5.72	0.0003	1	2.17	0.150
<i>D.cinerea</i>	6	1.53	0.189	1	6.53	0.014

Table 4.2 shows the results of a 1-way ANCOVA's of regrowth height performed for each species. In *A.karoo* there was no significant difference in regrowth height between different season of defoliation (Figure 4.1). Regrowth height was also independent of pre-clip height and time since clip. Mean regrowth height only exceeded pre-clip height following the May 1996 clip.

In *A. nilotica* there was a significant difference between height of regrowth after different seasons of defoliation (Figure 4.1). Mean regrowth height was also independent of pre-clip height and time since clip. Regrowth height exceeded pre-clip height following the September 1995 clip.

In *D.cinerea* height regrowth was poorer after the summer clips (i.e. Nov, Jan and March) but this difference was not statistically significant. Regrowth height was also independent of pre-clip height and time since clip. Regrowth height exceeded pre-clip height in September 1995. However the lack of statistical significance in the ANCOVA is most likely attributed to the influence of pre-clip height (see Figure 4.3).

4.4.1.2 Number of resprouting stems

Figure 4.4 shows the mean and standard deviation for pre-clip and regrowth number of stems for the three study species clipped in different seasons. The results from the 1-way ANOVA's used to determine whether there was any significant difference between treatments are shown in Table 4.3.

In the first year following clipping *A.karoo* produced approximately double the number of pre-clip stems except following the May 1996 treatment where fewer stems were produced. However there were no statistically significant differences between treatments.

In *A.nilotica* there was higher variation in the number of stems produced following different clipping seasons and this was statistically significant. The number of stems produced after the July 1995 clip was almost three times greater than the pre-clip number. In March and May of 1996 the number of stems was less than the pre-clip number (Figure 4.4).

In *D. cinerea* the variation in number of stems between treatments is not statistically significant. The lowest number of resprouting stems was produced after the summer clip (i.e. Jan 1996) and highest after winter (i.e. July 1996) and early spring (i.e. Sept 1996) clips.

Table 4.3 F ratios and significance levels from 1-way ANOVA's of number of resprouting stems and season of clip. Statistically significant results are shown in bold.

Effect	df	F	p-level
<i>A.karoo</i>	6	0.59	0.734
<i>A.nilotica</i>	6	5.25	0.0006
<i>D.cinerea</i>	6	1.09	0.3801

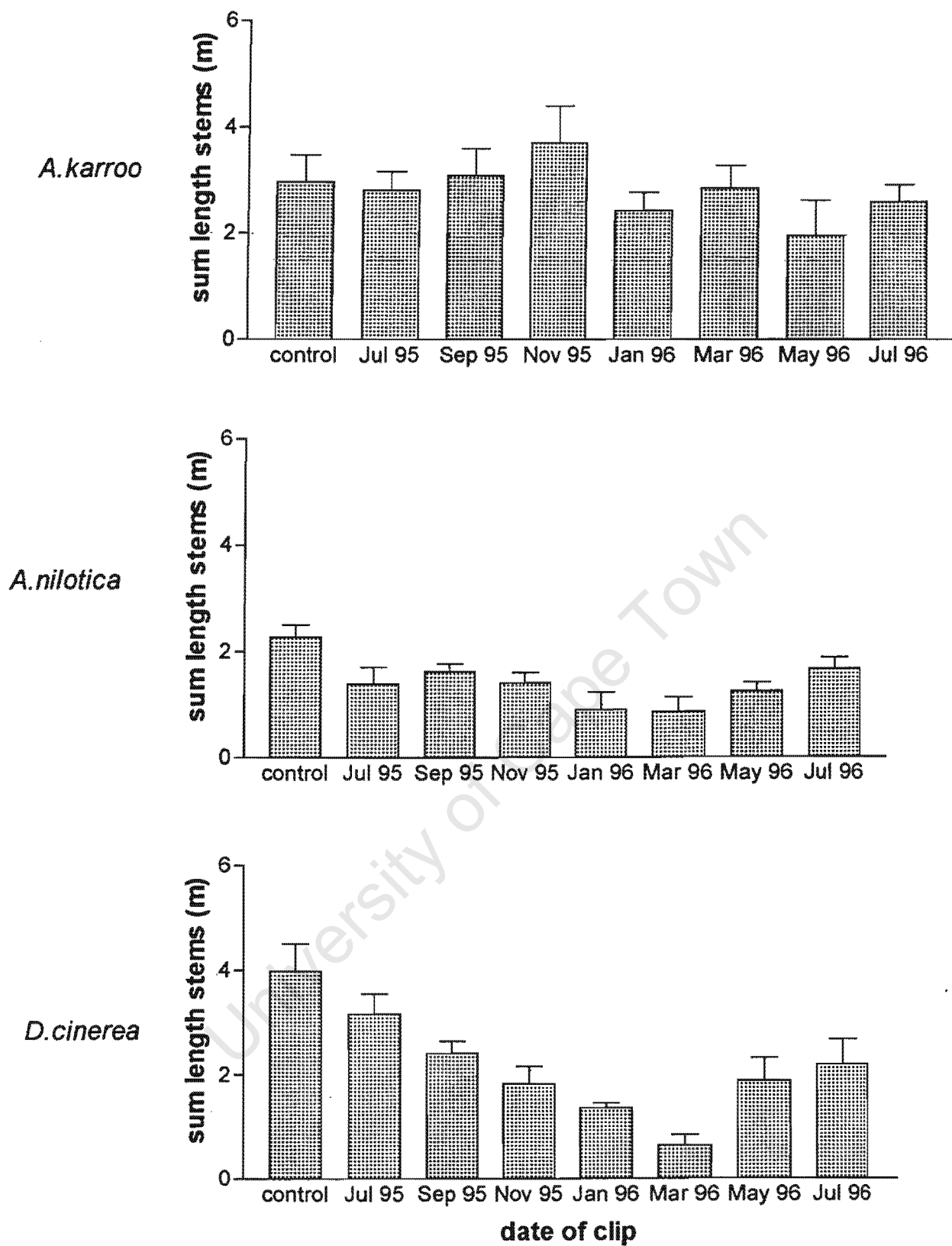


Figure 4.5 Sum of the length of resprouting stems (recorded in August 1997) in trees clipped at different times of the year between July 1995 and July 1996. Growth of controls is also shown. Data are means and standard deviations.

4.4.1.3 Sum of the length of resprouting stems

Figure 4.5 shows the mean and standard deviation of the sum of the length of all resprouting stems of the three study species clipped in different seasons. The results from the 1-way ANOVA's used to determine whether there was any significant difference between treatments are shown in Table 4.4.

There was no statistically significant difference in sum of the length of stem regrowth in *A.karoo* across different clipping seasons. The lowest regrowth response occurred after the May 1996 clip.

A.nilotica showed little variation in regrowth response across the different seasons of defoliation. The lowest regrowth response was produced following the summer (i.e. January) and early autumn (i.e. March) 1996 clips and this was statistically significant.

In *D.cinerea* there was a steady decline in regrowth response from mid winter clips (i.e. July 1995) through to a minimum in early autumn (i.e. March 1996) followed by a recovery in vigour for the May and July 1996 clips. The vigorous resprouting after these second winter clips was surprising since the treatments were applied just two months before all treatments were burnt. This indicated that time since clip had a minor effect compared to season of clip. Differences in re-growth vigour were statistically significant.

Table 4.4 F ratios and significance levels from the 1-way ANOVA's of the sum of the length of resprouting stems and season of clip. Statistically significant results are shown in bold.

Effect	df	F	p-level
<i>A.karoo</i>	6	0.47	0.824
<i>A.nilotica</i>	6	6.36	0.0001
<i>D.cinerea</i>	6	3.04	0.013

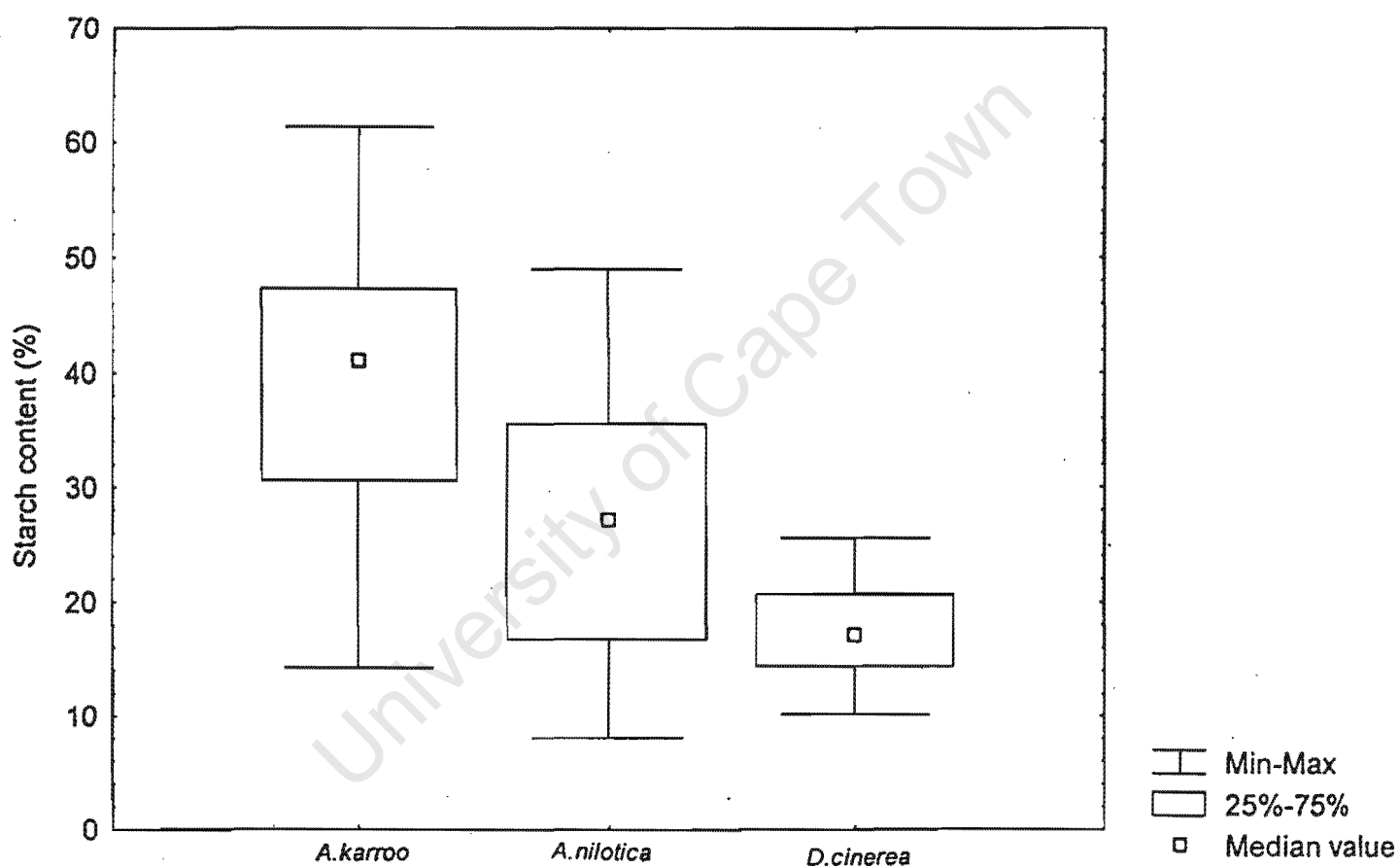


Figure 4.6 Median percentage dry weight root starch content determined from root samples collected every two months for one year for three study species. Box whisker plots show the min and max values, median value and 25-75% range of data points.

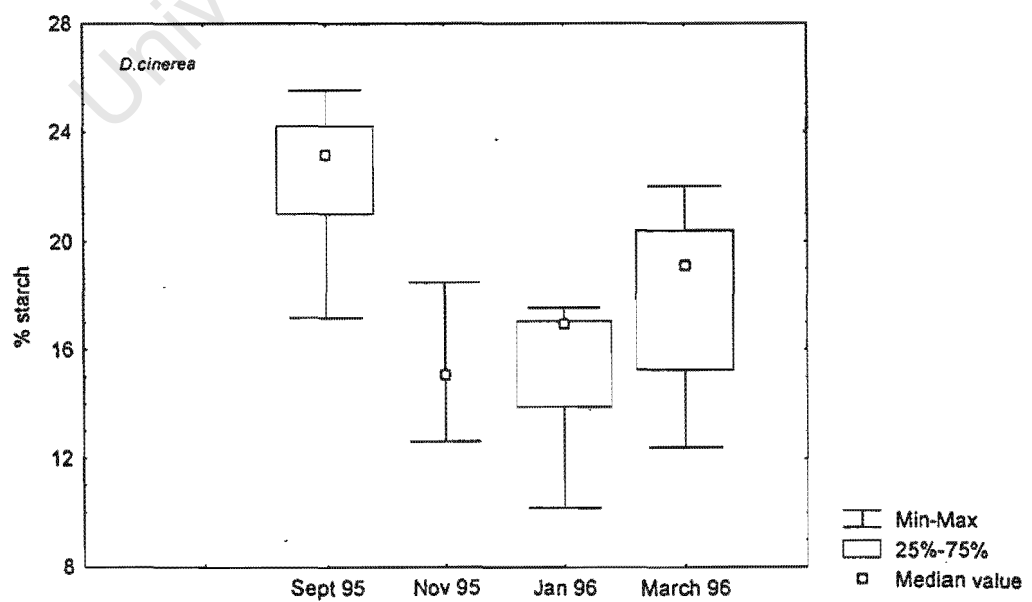
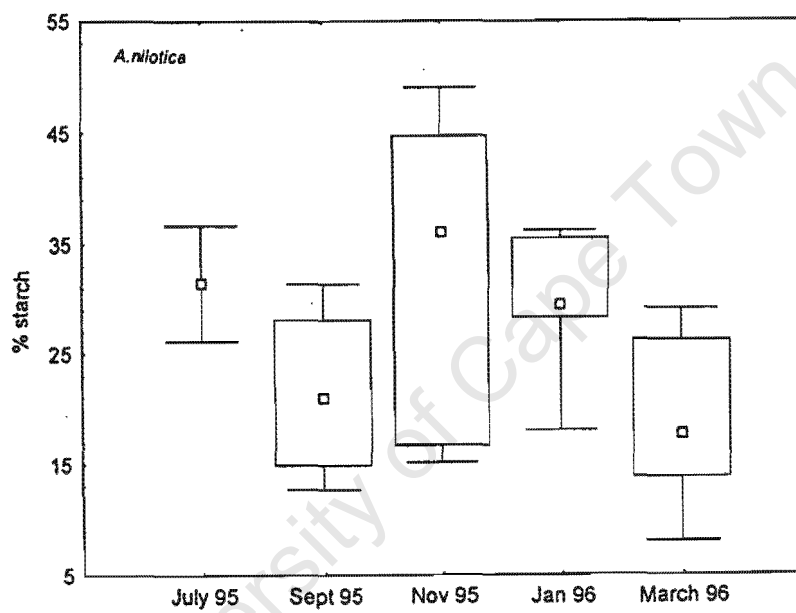
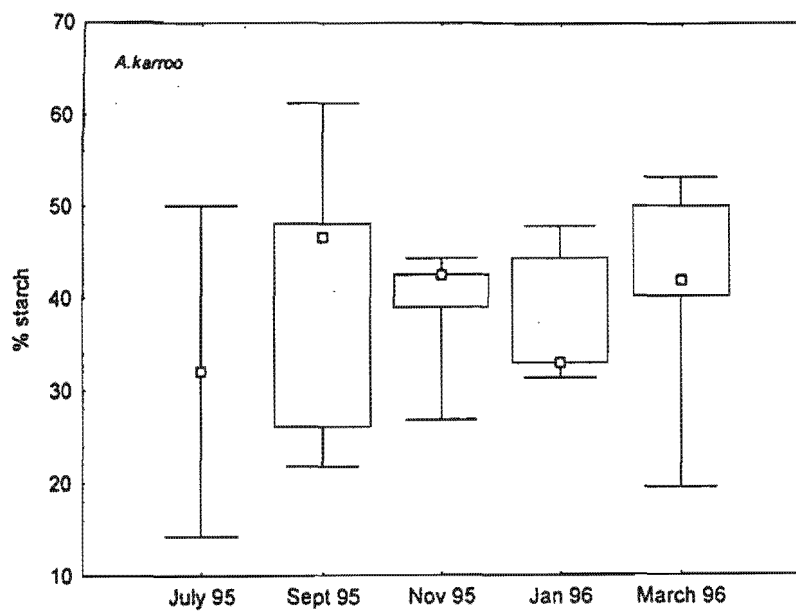


Figure 4.7 Seasonal variation in percent dry weight root starch content for three study species. Median % dry weight root starch content was determined for five individuals of each species every two months for one year. Box whisker plots show the min and max values, median value and 25-75% range of data points.

4.4.2 Phenology

Table 4.5 shows the phenology of each species at each clipping event during the experimental period. In *A. nilotica* and in *D. cinerea*, new leaves were initiated in late spring (November) and production continued through summer until March. Both species also flower from late spring and fruit over summer. *A. karroo* plants had new growth present at most dates *except* early spring and summer. However it flowered and set fruit at similar times to the other two species.

4.4.3 Starch analysis

The comparative root starch content of the three study species is shown in Figure 4.6. Overall *A. karroo* had the most starch (up to 60% dry weight), *A. nilotica* was intermediate (median of 28% dry weight) and *D. cinerea* has the lowest (median of 18% dry weight). Figure 4.7 shows root starch content at different times of the year for the three study species. *A. karroo* showed a high degree of variation within seasons, but little variation between seasons. *A. nilotica* showed some variation between seasons with highest content during early summer (i.e. Nov 1995) and lowest during Spring (Sept 1995) and early autumn (March 1996). *D. cinerea* showed the greatest variation between seasons with highest starch content in spring (Sept 1995) and lowest in summer (i.e. Nov 1995 and Jan 1996).

Table 4.5 Phenology of the study species at time of each clip. buds = flower buds, flowers, grn pods = green pods, dry pods = mature/dry pods, new = new leaves (gradual recruitment of new leaves), mature = mature leaves, old = old leaves, no leaves.

DATE	<i>A.karoo</i>	<i>A.nilotica</i>	<i>D.cinerea</i>
20 July 1995	new mature	mature	mature old
15 Sept 1995	new	old no leaves	no leaves
28 Nov 1995	buds flowers mature	new	flowers new mature
24 Jan 1996	buds flowers mature	new mature	new mature
26 March 1996	gm pods new mature old	new mature	new mature old
27 May 1996	gm pods dry pods new mature old	mature old	new mature old
29 July 1996	new old	mature	old no leaves
11 August 1997 (regrowth measurement)	new mature	new mature	new mature

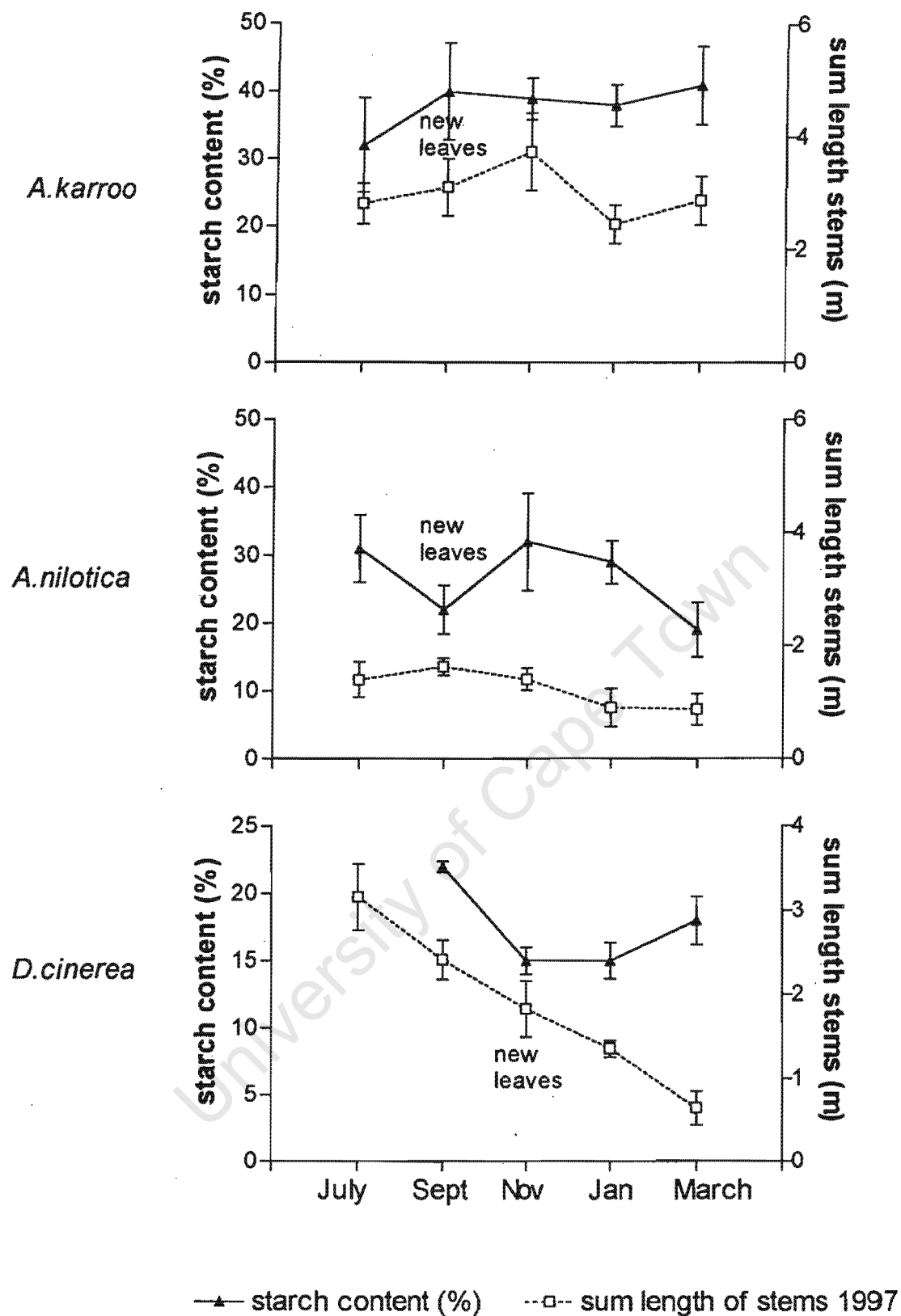


Figure 4.8 Variation in root starch content and sum of the length of resprouting stems recorded in August 1997 with change in season (July 1995 and July 1996). Data are means and standard deviations. The time when new leaves flushed is indicated.

4.5 Discussion

The three study species varied in their responses to defoliation in different seasons. Season of defoliation has little effect on the response of *A.karoo*. Only the early dry season treatment, which coincided with seed set, caused slightly reduced regrowth vigour in terms of number of stems and the sum of their length. When the results were compared with the same treatment and size class of clipped trees in Chapter 2 and 3, the observed response was very similar. Thus seasonal effects did not appear important in *A.karoo*. The size dependent response seen in Chapter 2 suggested that the pre-clip height class variation in *A.karoo* may have contributed to the results observed. In any future experiments investigating seasonal effects, trees in a narrower height class bracket should be selected. Response in *A.karoo* was most likely due to the very large root starch reserves that are rapidly mobilised for regrowth when a tree is injured. *A.karoo* populations elsewhere may however show higher sensitivity to season of injury (Teague 1988a and 1988b). Deciduousness may be a good predictor of variation in carbon reserves. In this study *A.karoo* was weakly deciduous, and never lost all its leaves during the period of study (Figure 4.8). However, *A.karoo* is more strongly deciduous in the Eastern Cape and was sensitive to defoliation in the early part of summer (Teague 1988a and 1988b).

A.nilotica and *D.cinerea* showed a significant difference in regrowth responses following defoliation in different seasons. Both species showed poorest regrowth after mid (Jan) to late summer (March) injury which compared favourably with response observed following winter and summer fires in Chapter 3. Of the three study species *A.nilotica* showed the most variation in regrowth response relative to the season of defoliation. In terms of height and sum of the length of resprouting stems, *A.nilotica* was most susceptible to defoliation in mid and late summer (January and March 1996). These regrowth results were consistent with those found following a controlled summer burn reported in Chapter 3 where *A.nilotica* showed reduced regrowth after a summer burn relative to winter burns.

A.nilotica did not flower in any of the height classes studied. Plants produced a new flush of leaves from November through to March which may have drained root reserves over the sensitive summer period (Figure 4.8). Root starch content was depleted, relative to November values, in the January and March analysis supporting the hypothesis that root

reserves are depleted after new leaf growth. The slightly lower starch reserves during January and March were perhaps due to allocation of reserves to general plant growth. In terms of regrowth height and number of stems produced, *A.nilotica* was least susceptible to defoliation during September 1995 which coincided with leaf loss. According to allocation theory (Bond and van Wilgen 1996), deciduous species have their highest root reserves at leaf loss, however this was not evident in the root starch results found in this study. This may have been due to the small sample size of roots used, or, that a more precise understanding of regions of root starch storage is required for a more accurate comparison. Phenology was a good predictor of tree sensitivity in *A.nilotica*, since new leaf growth coincided with poor regrowth following defoliation (Figure 4.8).

D.cinerea was most susceptible to defoliation in mid to late summer as measured by regrowth height and the sum of the length of stems. This was consistent with results from a summer burn (Chapter 3) when mortality was high and regrowth poor relative to dry season burns. The mid-summer period was a few weeks after the flush of new leaves and flowering in late November. *D.cinerea* was the most strongly deciduous of the three species studied and starch reserves were lowest in November and January, coinciding with the flush of new growth. A steady decline in regrowth vigour appeared to track a decline in starch storage (Figure 4.8). Phenology was therefore a good indicator of starch reserves and vulnerability to defoliation in *D.cinerea*.

The relationship between tree size and response is important to bear in mind when interpreting these results. Neither *A.karoo*, nor *A.nilotica*, invest significant resources in reproduction until they have grown above the zone of most fire damage. In contrast, *D.cinerea* reaches maturity entirely within grassland fire flame heights. The added burden of investing resources in reproduction might make this, and similar shrubby savanna species which mature within the fire trap, particularly sensitive to burning in the season when resources are most depleted by allocation to reproduction. The impact of allocation to reproduction on resprouting after different fire seasons should be considered in the design of any similar experiments in the future.

The different responses between the three study species may be partially explained by the gulliver life history described in detail in the following chapter. One of the possible mechanisms underlying this response is illustrated by the overall root starch storage

contents. The Acacias, especially *A.karoo*, have relatively high starch concentration in their roots relative to *D.cinerea*. High starch contents would be expected because of the need to build stems from stored reserves that can reach escape height before the next fire. This pattern may be expected in other pole forming species with gulliver type life histories such as *Brachystegia* species. *D.cinerea*, with no need to build tall stems, most likely relies on the current year's photosynthesis for recovery from injury. Other bush encroaching species that are shallow rooted and hard wooded such as *Dalbergia melanoxylon* and *Acacia mellifera* are expected to exhibit similar response.

Extrapolating these clipping results to fire management is complex since the practicalities of burning in summer to reduce problem species requires a careful assessment of the pre-burn vegetation composition and condition. For example in summer burns, high fuel moisture content often reduces fire intensity and levels of topkill which will affect burning objectives. There is also some degree of speculation as to whether the plant moisture in tree stems protects the aboveground parts from fire. Furthermore, wet season burns are traditionally seen as unfavourable and are thought to damage the grass sward, even though there is little evidence to support this (Hardy *et al.* 1999). Although fuel moisture is higher during the summer months, in the HUP there are occasional opportunities for summer burns as seen in Chapter 3 (Photo 11).

In terms of managing densities of *A.karoo*, fire season does not appear to be a viable option for the height classes studied. On the basis of this experiment, *A.karoo* appears to be insensitive to variation in fire season. However, it is also possible that a single "out of season" defoliation is not sufficient to illustrate seasonal effects. Rather, seasonal effects may only become apparent after several successive season treatments in species such as *A.karoo*.

These results suggest that mid to late summer burning *may* be of value in reducing regrowth of *A.nilotica* and *D.cinerea*. *D.cinerea* is particularly vulnerable to summer burns. Conversely managers wishing to encourage the growth of *A.nilotica* should avoid burning in January.

These results provide a good rationale for future research into the effects of season of burn on the tree and grass component. A rigorous test of season of burn effects is required

based on longer-term experiments and larger sample sizes. It is recommended that a 5-10 year or longer experimental burning programme be initiated to explain the potential of summer burns for tree control. This should be coupled with a study of possible negative effects on the grass sward.

The interesting difference in starch storage in roots of the three study species also suggests that further investigation is warranted. The significance of root starch in post injury shoot recovery following burns in different seasons could shed more light on the underlying mechanism of different resprouting strategies. A limitation to this study was that defoliation was limited to a single event. Is it possible for example to exhaust the starch reserves in *A.karoo* through repeated defoliation, and if so, could one simulate this through management techniques?

Any future work looking at the relative absolute reserve storage among different species should sample precisely at the end of the growing season just before leaf fall. Sampling at other times can result in artifactual interspecific differences as species vary in their phenology of carbohydrate reserve accumulation and expenditure (Kozłowski 1992).

4.6 Conclusion

The use of different seasons of burn to manage tree biomass in savannas has been neglected in South Africa, primarily because of concern for negative impacts on the grass sward (Everson and Tainton 1984; Tainton and Mentis 1984). However this study suggests that prescribed burns in the wet season could play an important role in controlling tree densities of some species. The grass component was not part of my study but there were no obvious negative impacts on sward composition after experimental summer burns. The costs and benefits of burning in different fire seasons now needs to be pursued with experimental trials at a scale relevant for savanna range management.

My results also indicate that fire season impacts some species and not others. In this study, the species with the lowest root starch concentrations (*D.cinerea*), responded most to growing season burns. Species with large root starch concentrations were relatively unaffected. Differences in starch concentration and season of burn response correspond

with life history differences among the three species. *D.cinerea* grows to maturity almost entirely within the zone of maximum fire damage, typically suffers 100% topkill (Chapter 3), and probably uses post-burn photosynthate to recover canopy area. *A.karoo* and *A.nilotica* both grow to maturity only after emerging to heights where the canopy is not destroyed by burning. To do so, they appear to require substantial root carbon reserves to build long enough stems between successive fires to escape topkill. These “gulliver” type life histories are discussed further in Chapter 5.

Thus, the use of fire season as a tool for managing tree biomass depends on the species of interest. Shrubby species may prove more responsive to judicious use of fire seasons than tree species that only mature above the fire trap.

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5 GULLIVERS: A DISTINCTIVE LIFE HISTORY STAGE IN SAVANNA TREES

(This chapter is co-authored by W.J. Bond and I and has been submitted for publication. I contributed 50% to the ideas, and the modelling and data is based on the work in this thesis.)

5.1 Introduction

Savannas are among the youngest of the world's vegetation formations. C4 grasses first appeared in the equatorial tropics about 8 My ago spreading polewards to reach their modern extent in the last million years (Cerling *et al.* 1997; Ehleringer *et al.* 1997). These grasslands replaced angiosperm-dominated forests which had existed since early Tertiary times (Wolfe 1985). A small group of forest species must have survived the novel grassland conditions. They and their descendants radiated to form the distinctive savanna tree floras of the present within the last few million years. Savanna tree floras are distinct and different from forests in the same regions. Most savanna species, and some genera, are endemic to savanna formations in Africa and South America (White 1976; Sarmiento 1983). Very few species occur in both forest and savanna. The savanna environment appears to have posed a strong evolutionary barrier to colonisation by trees of forest origins. What adaptations/exaptations are required for a tree to penetrate and survive successfully in savannas? In this chapter, we suggest that the very high disturbance frequencies associated with grassland fires were a major and distinctive selective barrier for trees and that many savanna tree species share similar and distinctive life history features that allow recruitment despite frequent fires.

C4 grasses, especially members of the sub-tribe Andropogoneae, frequently form tall tussock grasslands which dry out to form highly flammable fuels in the dry season. Fires in mesic savannas occur at intervals as short as 1 to 3 years (Trollope 1984, 1993; Sarmiento 1983; Bond 1997). Such frequent fires pose a major hazard for tree recruitment. Tree seedlings not only compete with grasses directly, but also have to survive repeated burning yet grow tall enough to eventually emerge from the grass layer. We argue that recruitment of trees, especially in mesic savannas, is limited less by the availability of seeds or seedlings than by opportunities for escaping from the zone in which fires are sufficiently intense to kill aboveground stems (i.e. topkill). Many savanna

trees have a distinctive set of adaptations that promote rapid height growth of juveniles out of zone of greatest fire damage. This results in a marked discontinuity between growth and reproductive patterns in trees above and within the flame zone. The distinctive nature of these features warrants a unique term to draw attention to the phenomenon. We suggest the word "gulliver" after Jonathan Swift's sailor cast ashore and bound down by thousands of tiny Lilliputians (the grasses) but a giant amongst them once he had escaped his bounds (see also Bond and van Wilgen 1996).

Gullivers are the juvenile phase of savanna trees which are prevented from escaping to become adults by frequent injury from burning (Photo 6-7). Trees may spend a greater part of their lives in this stunted state than as tall adult trees. The characteristic feature of gullivers is a marked discontinuity in growth and reproductive patterns above and below the critical height at which trees escape topkill. Gullivers appear to have distinctive demographic, morphological and physiological properties which merit special attention when dealing with the population biology of savanna trees.

Alternatives to gulliver-type life histories also occur in savannas. Relictual forest species persist in relatively fire-free sites in many savanna landscapes (e.g. *Celtis mildbraedii* and *Protorhus longifolia*). More interesting in terms of the evolutionary barriers imposed by fire-prone grasslands, are woody plants which survive frequent fires as shrubs. These grow and reproduce entirely within the fire zone. These non-gulliver, but fire-tolerant species, can become very common (e.g. *Dichrostachys cinerea* and *Acacia caffra*). A third option for coping with savanna conditions is shown by a peculiar set of African species. These are dwarfed forms of trees, with extensive woody branching below ground and little more than leaves appearing above-ground (e.g. *Dichapetalum cymosum* and a dwarf form of *Pseudolachnostylis maprouneifolia*). They are endemic to savannas (White 1976; Gillon 1983).

We discuss the demography, morphology and evolutionary biology of gulliver-type species below while giving some consideration to alternative life histories. Many of our observations are based on a study of the demography of savanna species in the Hluhluwe-Umfolozi Park.

5.2 Demography of gullivers

The information required for demographic studies of gullivers differs from standard demographic analyses of woody plants. Indeed much effort has been wasted on standard demographic analyses for these non-standard savanna life histories. To predict recruitment into tree size classes in gulliver-type species, one needs to be able to predict the frequency of escape opportunities. These are periods when fires are sufficiently far apart for gullivers to grow out of the fire zone. Savanna fires seldom kill juvenile trees (Rutherford 1983; Gillon 1983; Trollope 1984; Frost 1984; Chapter 3 this thesis). However they influence their architecture by killing above-ground parts. Within the flame height of grass fires, there is often complete "topkill" - the death of all above-ground stems. Plants resprout from basal burls or roots (Photo 4). Where topkill is incomplete, plants may coppice from surviving buds on the stem (Photo 3). Taller trees, above the fire zone, do not suffer topkill and plants continue to grow from pre-burn stems with no loss of height. The time required for gullivers to escape the fire zone can be estimated from information on **escape height**, and the **rate** at which species grow to reach escape height (Figure 5.1). Trollope (1984) has studied the former in some detail. For typical grassland fire intensities ($500-2000 \text{ kJs}^{-1}\text{m}^{-1}$), escape height is between 1.5 to 3m. The probability of topkill increases with increasing fire intensity but only for plants below escape height (Figure 5.2). The rate at which trees grow to reach escape height is a critical variable for estimating the frequency of escape opportunities for a given population. However despite its importance, we could find virtually no information on this rate in the southern African literature. Chidumayo (1997) followed height increments for several Zambian woodland species (Figure 5.3). His data suggest a discontinuity in height growth rates above and below escape height. Height increment is rapid below escape height (2-3 m) but much slower at or above it. All of these species grow to 10 m or more. We have seen a similar discontinuity in height increment, also at 2-3m in *Acacia* species in Zululand (Chapter 2-3 this thesis). Chidumayo's data suggests that an interval between fires of at least 6 to 9 years is required for these species to emerge from the fire zone. The data in this thesis suggest comparable periods to reach escape height. Regrowth rate is also known to increase with pre-burn plant size (Grundy 1994; Chapter 2 this thesis).

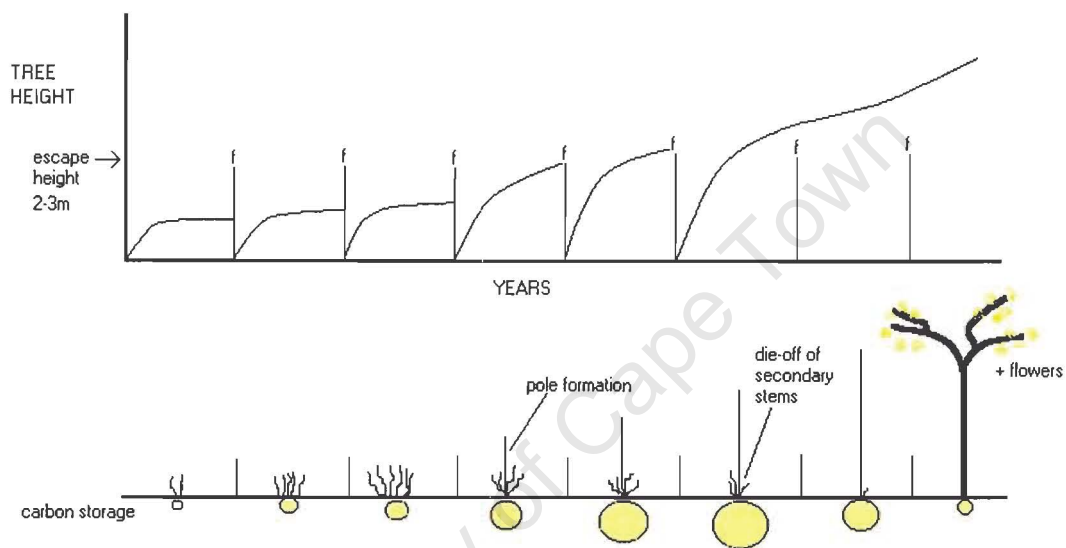


Figure 5.1. A hypothetical diagram of gulliver regrowth rates after successive fires (f) and escape height. The regrowth response is correlated with pole or dominant stem formation and carbon storage in the roots. The relative amount of stored carbon in the roots is indicated by the size of the shaded circles.

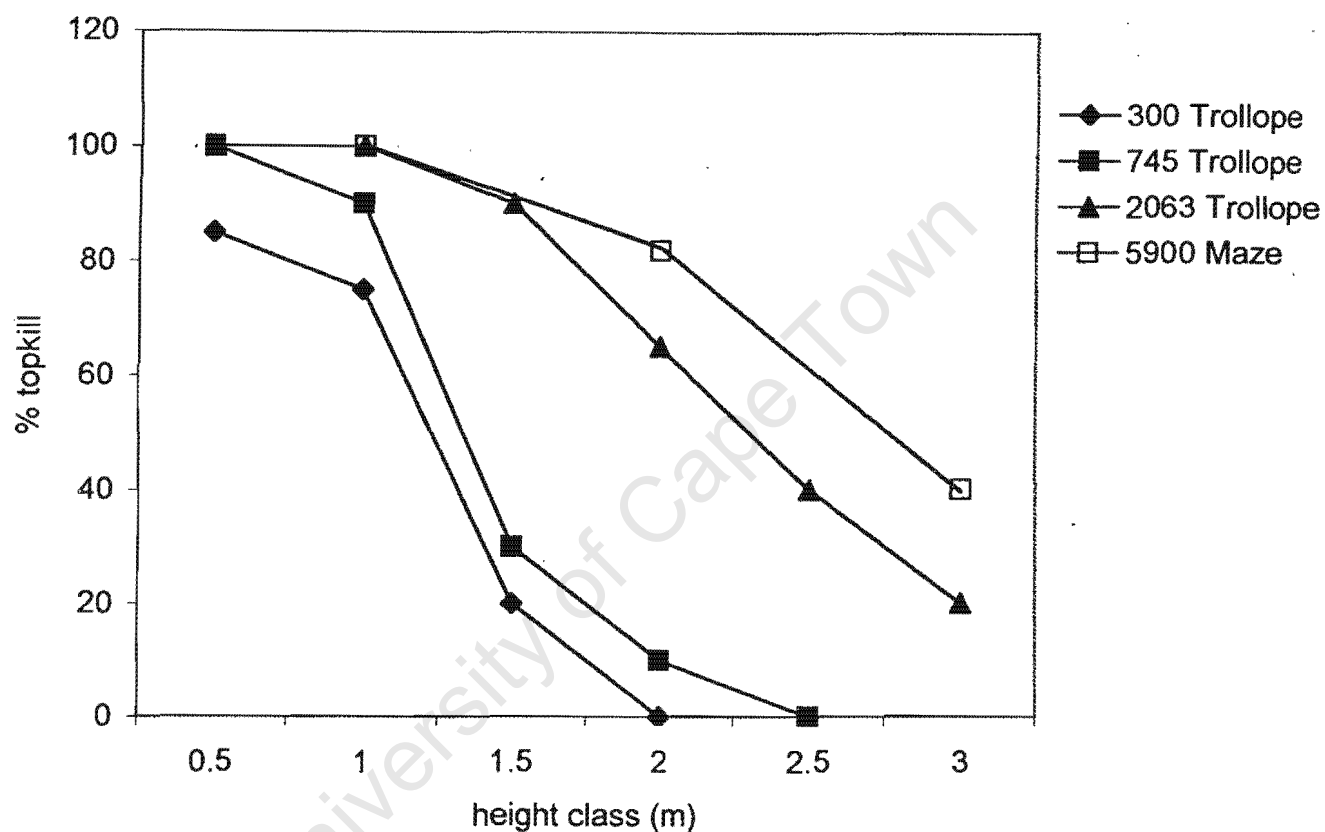


Figure 5.2. The relationship between plant height and topkill in *Acacia karroo* at four fire intensities. Topkill causes death of above ground stems and coppicing from the base. Data from Trollope (1984) and Maze (Chapter 3 this thesis). The labels for each line are fire intensity in kJ /s/m.

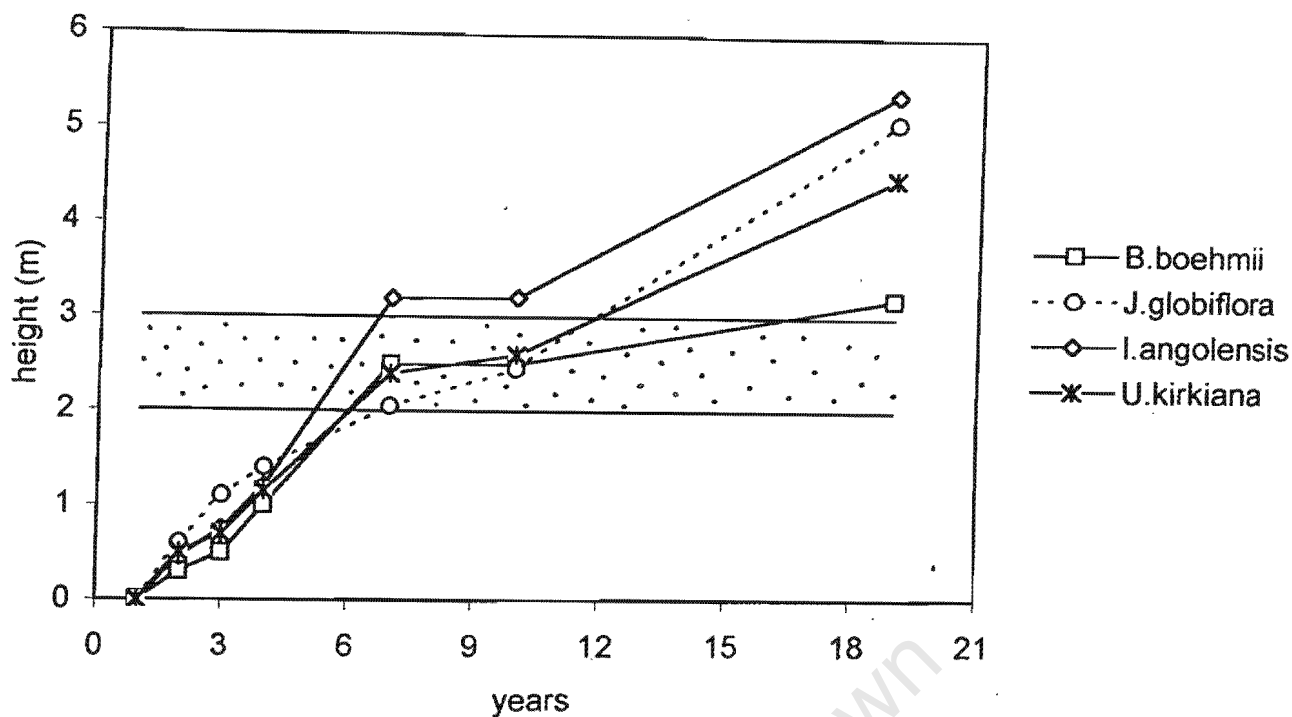


Figure 5.3. Height growth below, and above the fire zone for four Zambian savanna woodland species (data ex Chidumayo 1997). The height at which species escape topkill is hatched. Species are *Brachsytegia boehmii*, *Julbernardia globiflora*, *Isobertinia angolensis* and *Uapaca kirkiana*.

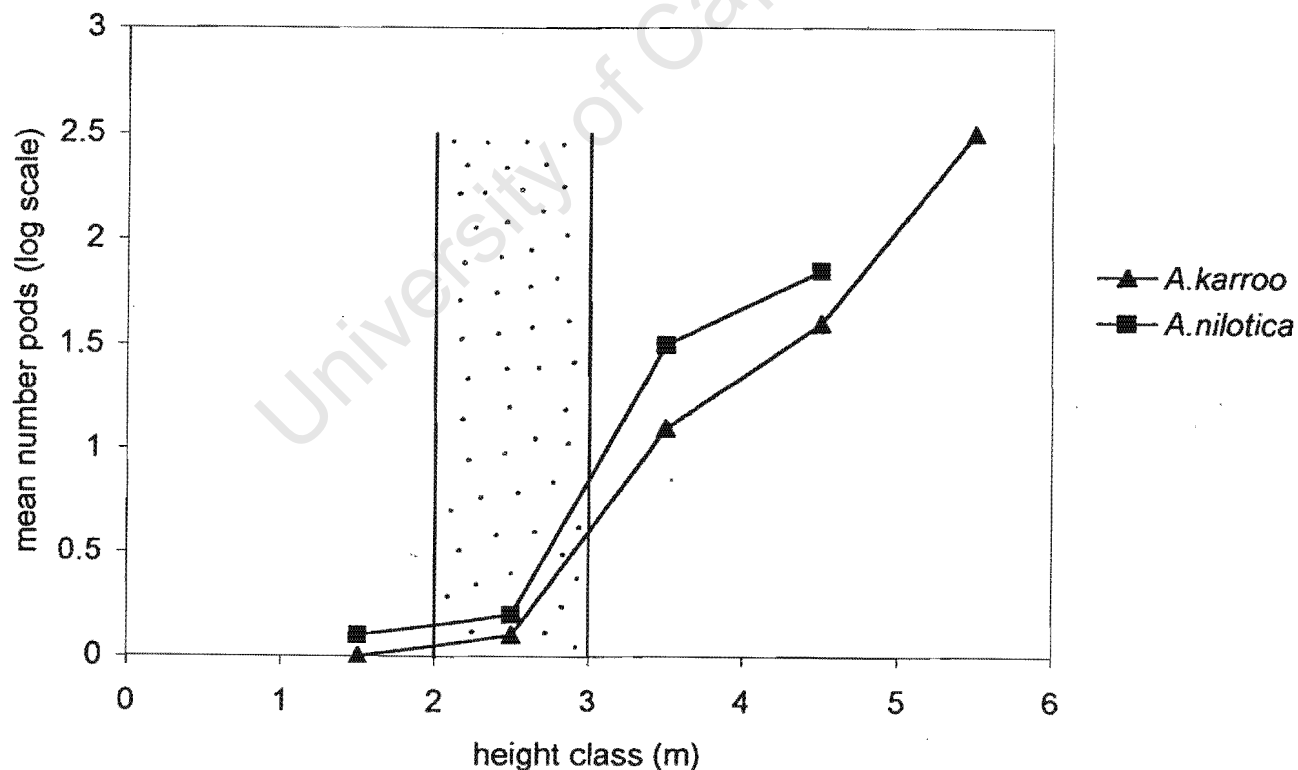


Figure 5.4. Pod production below and above fire escape height in *Acacia karroo* and *A. nilotica*. Savanna populations were sampled in Hluhluwe-Umfolozi Park. Pods were censused from ten plants in each size class. The vertical hatched bar represents the height at which species escape topkill.

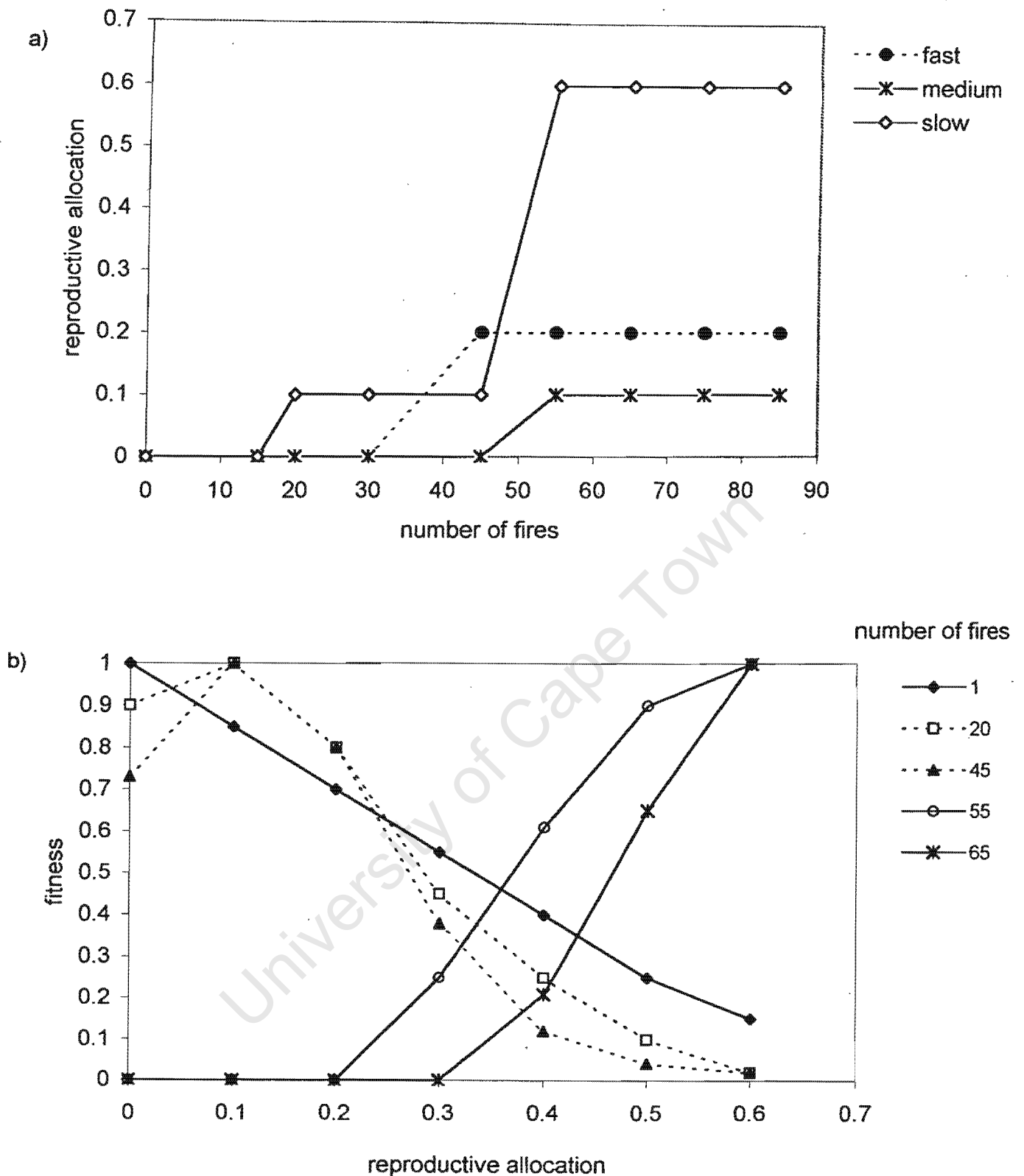


Figure 5.5. Results of a simulation study on fitness consequences of allocation to reproduction or growth in gulliver-type life histories. Figure a) shows the allocation level producing the most seeds (the evolutionary optimum) in relation to fire frequency for three different growth rates ($H_{mx}=10m$, $K=10$, $b=5$). Figure b) shows fitness, measured in relative seed production, in relation to reproductive allocation for a variety of fire frequencies for a simulated slow-growing species ($g=0.25m/y$). See text for model details.

Given information on escape height, topkill and rate of height growth, the probability of recruitment into larger size classes can be estimated from fire frequency and intensity. Both are strongly related to grass biomass. Grass productivity is, in turn, related to rainfall. Thus recruitment of gullivers into larger trees is a function of grass production and fire. For gulliver-limited recruitment, the transition from gullivers to larger size classes should be modelled as a function of fire. Subsequent growth can be modelled in a standard manner. Turnover of gullivers, at least in some species, is low. Menaut *et al.* (1990) reported gullivers persisting for 40 years or more for West African species. Trollope (unpublished) has followed the same *A. karroo* individuals in a 25 year burning experiment without observing mortality, reproduction or, indeed, escape above the fire zone over this period in his burning treatments.

The discontinuity of tree behaviour above and below escape height occurs not only in growth rate but also reproductive behaviour. Figure 5.4 shows pod production in two South African *Acacia* species. Pods were absent or very rare in plants <2-3m tall, but increased exponentially above this threshold height (Figure 5.4). *A. karroo* populations from semi-arid areas, which do not experience fire, produced pods from 1m plants and pod production varied more with canopy size than with height.

5.3 The morphology of gullivers

The ability to sprout after injury (such as that caused by burning) is probably an ancient trait in angiosperms (Wells 1969; James 1984). Many woody species have lost the ability to sprout in fire-prone woodlands and shrublands (eg. many members of the Proteaceae in Mediterranean shrublands, Bond and van Wilgen 1996). All savanna trees sprout after fire, especially in the juvenile phase, as do many forest species that are never exposed to fire. The distinctive feature of savanna trees is their ability to take on a geophytic habit, while their aerial parts are repeatedly destroyed by fire (Glover 1968). Seedlings are able to sprout within a few months of germination. They form multi-stemmed shrubs resprouting after each fire. In many species, a basal burl or lignotuber-like swelling develops at the junction between root and shoot (Boaler 1966; Glover 1968; Gillon 1983; Timberlake and Calvert 1993) (Photo 13). Similar structures are well-known in mediterranean-type shrublands (eg. James 1984) where, at least in some species, they

form as a normal ontogenetic feature and not as a wounding response (Carr *et al.* 1984). Their development and ontogeny has not received the same attention in savanna trees (Frost 1984; Lacey *et al.* 1982). The function of lignotubers is disputed (James 1984) but recent studies show that, in some species, they are important carbon storage organs which facilitate sprouting after injury, including fire (Canadell and Lopez-Soria 1998). Our studies of savanna trees in South Africa show that some species also accumulate large starch reserves in swollen roots in savanna environments. *Acacia karroo*, for example, accumulates up to 60% dry weight of TNCs in the root burl (see Table 4.1, Chapter 4).

The starch reserves may be a significant factor in the next, and most distinctive phase, of gulliver recruitment. Once some threshold size has been reached, a marked asymmetry develops among resprouting stems. One stem usually grows taller and more vertically than all the others forming a pole like structure that "bolts" and eventually the shorter secondary stems die (Chapter 2). If the pole is top-killed by fire, the plant resprouts again from the base, a similar asymmetry of shoots develops, and another pole is produced. In South African *Acacia* species, pole-forming gullivers reverted to the shorter multi stemmed form after three successive intense burns (Bond, Smythe and Balfour in press). Survival of the pole form through a fire depends both on variation in fire intensity (Trollope 1984) and particular tree characteristics. Recently Gignoux *et al.* (1997) described two alternative strategies in the pole stage for West African species. In the first, poles are heavily insulated with thick bark, reducing the risk of topkill in every fire. These thick-barked forms are usually slow growing. Species in the second group have thin bark, are poorly insulated from fire heat, but grow very rapidly. Gignoux *et al.* (1997) argue that the ability to grow rapidly itself ensures some insulation since thicker stems conduct less heat.

Similar alternative strategies occur in South African savanna species (this thesis). Observations of acacias in Hluhluwe-Umfolozi Park suggest that thick-barked forms often coppice from above-ground after a fire and reach escape height by repeated coppicing from pre-burn stems (e.g. *Acacia nilotica*), whereas thin barked forms are more likely to grow to escape height from basal sprouts in a single fire interval (e.g. *Acacia karroo*). Both alternatives are common (unpublished observations) and the relative advantage of each under different circumstances is unknown. However the key attribute of savanna species that allows recruitment to the tree layer, despite frequent

intense grass burns, is very rapid height growth during the gulliver stage from a geophytic root base. This is effected by the developmental switch from multi to single stemmed sprouts and rapid growth of the pole stage to escape height. Rapid height growth in the pole stage is dependent on accumulation of several years of stored carbon in the roots but we know of no physiological studies of the phenomenon. The geophytic character of gulliver-type species is apparent in our data for South African species (Table 5.1). *A. karroo*, a species that can form a 2m pole within 2 years of being burnt, had root starch reserves averaging 40% dry weight. *A. nilotica*, a thick-barked species which has slower height growth after fire, had starch concentrations of 26% in the roots. *Dichrostachys cinerea*, a multi-stemmed non-gulliver that does not emerge from the fire zone, does not develop a distinctive burl, and had the lowest starch concentration of the three species (16%). Shrubby forms that spend their entire lives within the fire zone need less stored carbon since they do not produce the pole stage to escape the fire zone.

Table 5.1. Mean starch content roots sampled from 30 individuals, sampled at five periods between 1995 and 1996. See Chapter 4 for analytical methods. *A. karroo* and *A. nilotica* are both gullivers (adults reach heights of 15m and 6m respectively) whereas *D. cinerea* is a non-gulliver (adult heights up to 2.5m).

	<i>A. karroo</i>	<i>A. nilotica</i>	<i>D. cinerea</i>
Starch content mean %	40.5	26.5	16.2
Range	12-61	8-49	10-25

Lignotuber-like structures disappear in adult savanna trees that we have observed. It seems likely that starch reserves in roots would also decline once trees have escaped the fire zone but no information is available. The failure of adult *A. karroo* and *A. nilotica* to sprout after decapitation (Chapter 2) might partly be a result of loss of stored root reserves due to mobilisation for growth once plants have escaped the fire trap. This is a topic for further research.

5.4 Life history evolution in gullivers

Life history theory for plants growing in fire-prone environments in general, and savannas in particular, has some novel aspects (Bond and van Wilgen 1996). Clark (1991) has developed models for sprouting and non-sprouting trees showing that they maximise different quantities from those usually considered in life history theory. Life history evolution in gullivers is interesting because of the decoupling of juvenile and adult phases. Because selection pressures are so different in adults and juveniles, allocation trade-offs may differ in gulliver and adult phases. General life history patterns of correlated growth, maturation time and lifespan (eg. Loehle 1988; Harper and White 1974) may not apply in these trees.

Allocation trade-offs in gullivers can be expressed in rates of height growth. Species that allocate carbon to thick, insulating bark should have slower growth rates, reducing the rate at which they reach escape height if they are subjected to intense burns. Plants that allocate resources to reproduction before they have reached escape height, would also trade-off height growth and the probability of escaping the next fire. Given that gullivers may spend decades in the fire zone before escaping, why stay a gulliver? Why not begin reproducing within the fire zone? Some *Acacia karroo* populations in the Hluhluwe—Umfolozi Park do indeed show precocious pod production, while still in the fire zone. Adults trees are very rare yet gullivers are common and widespread in the landscape. Gullivers that begin to reproduce precociously may be favoured by natural selection where fires are very frequent. To explore the conditions under which gulliver type recruitment is favoured over precocious reproduction in the fire zone, we developed a simple model of gulliver-type recruitment. The model was based on data from our Hluhluwe studies of *Acacia karroo*, *A. nilotica* and *Dichrostachys cinerea*. These are fast growing and slow growing gullivers and a non-gulliver (reproducing in the fire zone) respectively. The objective of the model was to determine optimum allocation patterns to growth or reproduction under varying fire regimes. We wished to determine when gulliver type life histories (i.e. deferring reproduction until plants have escaped the fire zone) would be favoured over precocious reproduction within the fire zone.

The model simulated fitness, measured in seed output over a 100-year period, for species with different rates of height growth and different patterns of reproductive

allocation against a background of changing fire frequency. Note that growth is always measured in **HEIGHT**, and not in terms of biomass.

Following Higgins *et al.* (2000), stem growth rates were simulated as:

$$h = h_t + (1 - h_t/h_{max})g \text{ in non-reproductive trees and}$$

$$h = h_t + (1 - h_t/h_{max})g(1-r) \text{ for reproductive trees}$$

where h = height increment, h_{max} is the maximum tree height (m), g is the maximum growth rate of stems (m/yr) and r is the fractional allocation to reproduction.

Reproduction was zero below a threshold height increasing exponentially thereafter:

$p = 0$ if $h < h_a$ where h_a is the height of first reproduction, and $h_a = h_t(1-r)$ where h_t is 2.5 m, the escape height.

$$p = K.h^b \text{ for } h > h_a$$

where p is number of seeds, K and b are constants. The form of the relationship and the values used for K and b used in the simulation approximated results for South African *Acacia* species (Figure 5.4).

Fires were simulated if a random number in each simulated year fell below some fixed value in a 100 year simulation. The 100 year simulation was repeated 50 times for each set of parameter values.

The results of the simulation are shown in Figure 5.5a and 5.5b. Figure 5.5a shows which reproductive allocation levels are most fit for a given fire frequency. The qualitative patterns are much the same for a wide range of reproductive values ($K = 10$ to 100 , $b = 1.5$ to 5) and results of only a single set of simulations are shown. Optimum allocation patterns vary with fire frequency and growth rate. For fast and medium growing gullivers, the fittest strategy was to allocate all resources to growth at lower fire frequencies. At higher fire frequencies, bet-hedging with some allocation to seeds is the fitter strategy, presumably as escape opportunities become rarer. The cost of reproductive allocation,

expressed as reduced height growth and therefore reduced probabilities of escaping the fire zone, is less in fast growing forms favouring somewhat greater allocation to reproduction at higher fire frequencies. In slow growing species, the gulliver strategy was unstable. At low fire frequencies, low allocation to reproduction in plants below escape height is the fittest strategy (figure 5.5b). As fire frequencies increased, there is an abrupt change in the optimum allocation strategy to maximum possible allocation to reproduction. In other words, slow growing species should adopt for life within the fire zone in mesic savannas with frequent fires because escape opportunities become so rare. *Dichrostachys cinerea* in the Hluhluwe-Umfolozi Park fits this pattern.

This result seems reasonable in the context of savanna ecology but would not be anticipated from general life history theory. Slow growing trees are usually slow maturing with long lifespans (eg. Loehle 1988). Our results suggest that slow growing trees would be forced to mature precociously in a fire-prone system because of the rarity of escape opportunities. They also suggest an explanation for the paradox that some of the most invasive non-gulliver shrubs in southern African savannas have very dense wood implying slow growth and long life spans rather than weedy, invasive characteristics. *Dichrostachys cinerea*, for example, is a widespread species that shows marked weedy tendencies and is a problem species in many rangelands. It is a multi-stemmed non-gulliver that fruits within the fire zone. It also has much harder wood than either *A. karroo* or *A. nilotica* (van Wyk 1984). If slow height growth is generally associated with dense wood (eg. Loehle 1988), our model predicts that species with dense wood would generally be shrubby non-gullivers in frequently burnt savannas.

5.5 Discussion

Savanna trees cope with a novel set of selective pressures different from those of their forest ancestors. The recent spread of fires into fragmented tropical forest has led to a number of studies on how forest trees cope with fire. Bark thickness appears to be a particularly useful predictor of which species survive, and which are eliminated by forest burning (e.g. Uhl and Kauffman 1990). Enough variation in bark thickness exists among forest species for many unrelated taxa to survive as savanna trees if this were the only obstacle for entering fire-prone grassy vegetation. We have argued that recruitment in the face of frequent fires is a major obstacle to colonisation of grass-dominated

vegetation. The morphology of grasses allows rapid recovery from burning but might also have allowed higher disturbance frequencies in terrestrial ecosystems than any other agent prior to human agricultural activity. Savanna trees have evolved a distinctive life history to cope with these disturbance frequencies. Juvenile forms have developed the ability to survive frequent fire and grow out of the fire zone within the short fire-free interval by using accumulated carbon stores in lignotuberous roots.

It is interesting to note that "geophytic" trees with a bolting habit also occurs among gymnosperms. Longleaf pine, *Pinus palustris*, is a well-known example from the southeastern United States. It also grows in savanna-like vegetation which has frequent fires. It has a gulliver-like stage which has also been interpreted as an evolved response to frequent fires (Wahlenberg 1946). *Pinus merkusii*, a tropical species, has a similar gulliver stage in savanna forms but not on the island of Sumatra where fires are rare (Stott 1988). These bolting pines differ from angiosperm savanna trees, however, in that the latter are able to repeat the process many times.

Savannas, especially in Africa, are home to numerous browsing mammals. Though browsing may act with fire to slow the emergence of trees from juvenile to adult stages (eg. Dublin *et al.* 1990; Pellew 1983) it is unlikely to have selected for gulliver type recruitment. Browsing pressure, unlike fire, is a feature of both forests and savannas and is unlikely to have produced a selective barrier for tree entry into grasslands. Gulliver type architectures, especially the pole-stage, do not seem to provide effective defence against mammalian herbivory. In contrast, multi-stemmed dense canopies characterise some of the most browsing tolerant savanna trees. Low densely branched canopies form formidable cage-like structures armed with spines or prickles in the more browse-tolerant African acacias (eg. *A. drepanolobium*, *A. tortilis*). This architecture is the opposite of pole-forming gullivers in fire-prone grasslands. The distribution of gulliver-type species is also not congruent with browsing mammals. Mammal densities are lowest, and browsing species fewest, in frequently burnt mesic savannas like the miombo woodlands of central Africa (McNaughton and Georgiadis 1986) where gulliver type life histories are common (Glover 1968).

We predict that gulliver type life histories will be most common in mesic savannas which are subjected to frequent fires. In arid savanna, populations may be limited more by

years of sufficient rainfall to produce seeds or allow successful seedling establishment. Cohorts of plants are more likely to date from unusual rainfall in arid savannas, and unusually long intervals between fires in mesic savannas (Higgins *et al.* 2000; Bond and Midgley 2001).

Gulliver-type recruitment may be but one factor allowing tree colonization of C4 grasslands since their appearance in the late Tertiary. There is still a great deal to explore on how trees and other life forms coped with this new environmental setting. We note that recent studies suggest that the origin and spread of C4 grasslands may owe more to declining levels of atmospheric CO₂ in the late Tertiary than to climate change (Ehleringer *et al.* 1997; Cerling *et al.* 1997). It seems highly likely that low CO₂ levels would also have slowed tree growth rates, including recovery after fire, relative to early Tertiary times. The recruitment problem for trees in frequently burnt grasslands would be exacerbated in a low CO₂ world aiding the spread of grassy vegetation into formally forested areas (Bond and Midgley 2000).

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6 CONCLUSIONS AND MANAGEMENT IMPLICATIONS

6.1 Key research findings

This thesis has shed some light on an area of savanna ecology that has been largely neglected in South Africa. It has, however, only scratched the surface of understanding the variation in tree response to fire, and the underlying causes. The key findings of this thesis can be summarised as follows.

Savanna trees exhibited marked differences in response to injury by clipping and fire (Chapter 2 and 3). The variation was found within and between species, from arid to mesic sites and across different fire seasons. All four study species had the ability to resprout at a very early age (i.e. at 6 months) and this ability was retained and improved with tree height, until maturity when sprouting ability rapidly declined. *Acacia caffra* adults were an exception in that trees retained resprouting ability through to adulthood. In addition to variation in the resprouting ability of trees, an understanding of the vigour, or rate of resprouting, is critical for predicting the frequency of escape opportunities. This study found that regrowth vigour of injured or topkilled trees followed a similar size dependent pattern but the regrowth rates differed among species.

Trees also responded differently following injury in summer versus winter. Summer burns, an uncommon burning practice in these reserves, killed substantial numbers of *A.nilotica* and *D.cinerea*, but not *A.karoo* (Chapter 3). Mortality was higher after summer burns than in the “normal” winter burns in the dormant growth season. One of the possible mechanisms underlying this response is the overall root starch storage contents (Chapter 4). The Acacias, especially *A.karoo*, have relatively high starch concentration in their roots relative to *D.cinerea*. The species with the lowest root starch concentrations (*D.cinerea*), responded most to injury in the growing season. Species with large root starch concentrations were relatively unaffected.

Differences in starch concentration and season of burn response correspond with life history differences among the three species. *D.cinerea* grows to maturity almost entirely within the zone of maximum fire damage, typically suffers 100% topkill, and probably uses

post-burn photosynthate to recover canopy area. *A.karoo* and *A.nilotica* both grow to maturity only after emerging to heights where the canopy is not destroyed by burning. To do so, they appear to require substantial root carbon reserves to build long enough stems between successive fires to escape topkill (Chapter 4). *D.cinerea*, with no need to build tall stems, most likely relies on the current year's photosynthesis for recovery from injury. *A.nilotica*'s strategy differs slightly to *A.karoo* in having a slower regrowth rate, however, it eventually manages to escape the flame zone by having much thicker bark than *A.karoo* and *D.cinerea*, and can withstand topkill to a greater degree (Chapter 3).

Two distinct life histories, gulliver and non-gulliver, are developed to distinguish the species in this study (after Bond and Van Wilgen 1996; Chapter 5). Gullivers are the juvenile phase of savanna trees which are prevented from escaping to become adults by frequent injury from burning. Trees may spend a greater part of their lives in this stunted state than as tall adult trees. The characteristic feature of gullivers is a marked discontinuity in growth and reproductive patterns above and below the critical height at which trees escape topkill. *A.nilotica* and *A.karoo* display typical gulliver type life histories where juveniles start as multi-stemmed and eventually emerge from the fire zone as single stemmed trees. Adults lose their sprouting ability. The non-gulliver type species, *A.caffra* and *D.cinerea*, survive to maturity within the flame zone, and remain multi-stemmed throughout. *A.caffra* retains vigorous sprouting ability when mature whereas *D.cinerea* loses this ability. Multi-stemmedness in adult trees may be a clue for distinguishing the gulliver versus non-gulliver life-history and should be further tested in other species and systems.

Gulliver type life histories are expected to occur mainly in mesic savannas which are subjected to frequent fires. In arid savannas, populations may be limited more by years of sufficient rainfall to produce seeds or allow successful seedling establishment. Cohorts of plants are more likely to date from unusual rainfall in arid savannas, and unusually long intervals between fires in mesic savannas (Higgins *et al.* 2000; Bond and Midgley 2001).

These life history differences provide useful insights into understanding savanna functioning at the level of the individual and have implications for management which are discussed in the following section.

6.2 Management recommendations

Fire is the principal management tool used to influence the density and architecture of the tree layer in savannas. The application of fire in South African savannas has been based chiefly on research into the effects of fire in the grasslands of the Natal Midlands. Grasslands respond best following winter or spring fires. Other more costly methods of managing the tree – grass balance in savannas include “dragging” (i.e. tractor dragging heavy chains or poles along the veld), manual cutting and herbicide spraying (Watson, 1995; Hoffmann *et al.* 1999). However, in many parts of southern Africa, these efforts are ineffective. One of the limiting factors in prescribing suitable management for bush encroachment is the lack of understanding on how trees respond to different types of disturbance or injury, both within and between species. My findings on the responses of the four species used in this study, as well as the gulliver – non-gulliver life history categorisation which may provide a short cut for predicting response of other species, provide useful insights for management.

However, there are limitations in extrapolating these findings into firm management recommendations since this study only investigated tree response following individual fires. The problem with this is that the responses observed may not be indicative of the longer-term effects of a fire regime of fires of that type. I expect that the cumulative effect of any fire regime is not simply the sum of effects of individual fires but rather an iterative effect. Another limitation is the effect of different fire regimes on the grass layer. The grass component was not part of my study, and although there were no obvious negative impacts on sward composition after experimental summer burns, this should be investigated quantitatively. Care should also be taken when extrapolating my findings to other areas where different subspecies or ecotypes occur. This is particularly so in the case of *D.cinerea* and *A.karoo* whose growth forms and subspecies look, and appear to behave, quite differently within a 80km radius of the HUP. Bearing these shortcomings in mind, I make the following management recommendations:

1. **Explicit vegetation management goals**

Whether managers wish to reduce the density of undesirable species or increase the density of others, they should be explicit about veld management goals. This may be viewed by some as obvious, however, from my interaction with managers and

researchers, I found that fire management was frequently applied without a clear goal. Being explicit about the desired vegetation structure or architecture and density of a target species, whether desirable or undesirable, will determine the management approach to some degree. Another frequent problem in fire management approaches is that they are often planned from year to year rather than over a longer-term. However, as previously mentioned, it may take several fires for the effects to manifest visibly in the tree layer. An understanding of the time scale and the process of progressively weakening trees must be stated up front.

Management goals and prescribed burning programmes should consider the following factors explicitly:

- i) the average rainfall as it determines the frequency and intensity of fires;
- ii) the species of concern and, if possible, its life history type; and,
- iii) the average height of trees in the stand.

2. Species differences

It is important to recognise that different species may respond differently to a prescribed fire and that this may depend on the life history of that species. For established intermediate sized trees it is important to identify the "problem species" as having gulliver or non-gulliver type life history, (i.e. some of the short cuts to establishing this are whether or not the tree matures within the flame zone, multi-stemmedness, and bark thickness).

3. Tree size

Fire is a two pronged recruitment bottleneck. Firstly, fire limits recruitment and growth of seedlings, and secondly, it limits recruitment of gullivers in to the canopy. Fire may cause different levels of mortality and topkill in the tree layer dependent on tree height. An understanding of the height dependent response curves (mortality, topkill and regrowth vigour) for each species will be critical for prescribing fires. Based on the results of this study one can predict the heights most resilient and susceptible to injury. Adult mortality would be high due to elephant damage in *A.karoo* and *A.nilotica*, and similarly following wood harvesting by humans. However, for the management of bush encroachment (i.e. usually trees in the intermediate height classes), the emphasis on mortality in savanna research and management may be inappropriate since mortality occurs in a relatively

small proportion of trees in a stand. This is also acknowledged by Trollope (1984 and 1998) in South Africa but is not yet widely accepted.

4. Rainfall

Rainfall pattern, which is the key determinant of the fuel load, will determine what time of year and how frequently prescribed burns can take place. In mesic savannas where sufficient fuel is produced, the options for designing a burning programme are more flexible than in more arid areas. In more arid areas, herbivores are likely to play a bigger role in controlling tree densities (Higgins *et al.* 2000).

5. Fire intensity

In the HUP high fire intensities can kill *A.nilotica* and *D.cinerea* but not *A.karoo*. Burning to maximise topkill and prevent increased woody biomass may be the only option for *A.karoo* in the HUP. The escape height (of decreasing probability of topkill) was ca 2.5m in *A.karoo* but less (only 1.5 m) in *A.nilotica* due to its thicker bark. Regrowth after topkill varied among species with tree height. *D.cinerea* was always topkilled and although burning for topkill is not a particularly effective method for controlling densities of this species, it will influence biomass. The practice of aiming for high intensity burns should be re-considered depending on the average height of gullivers. *A.karoo* growth may be retarded more by low intensity burns than high intensity ones where most plants are in smaller size classes (<1.5m).

6. Season of burn

The use of different seasons of burn to manage tree biomass in savannas has been neglected in South Africa, primarily because of concern for negative impacts on the grass sward (Everson and Tainton 1984, Tainton and Mentis 1984). Managers in HUP were very reluctant to burn in summer when this project was initiated, with most being skeptical about the effects. However my results, particularly the fact that topkill is readily achievable, indicate that summer burns may well be an effective option for managing densities of certain tree species. The use of fire season as a tool for managing tree biomass depends on the species of interest. Shrubby species (non-gullivers) may prove more responsive to judicious use of fire seasons than tree species that only mature above the fire trap (gullivers).

In the HUP fire season does not appear to be a viable option for managing densities of *A.karoo*, however, seasonal effects may only become apparent after several successive season treatments. In *A.nilotica* and *D.cinerea* mid to late summer burning *may* be of value in reducing regrowth. *D.cinerea* is particularly vulnerable to summer burns. Conversely managers wishing to encourage the growth of *A.nilotica* should avoid burning in January.

6.3 Recommendations for future research

The following questions have arisen from my research and warrant future research attention:

1. Does the gulliver vs non-gulliver life history characterisation account for a broad range of savanna trees?

The species differences exhibited in this study provide a basis for investigating life histories of other key woody species in more detail. Species differences should also provide a basis for re-examining coexistence modeling approaches. Future modeling efforts should attempt to move away from generalising the response of the tree layer, and rather focus on life history differences.

2. What are the costs and benefits of burning in different seasons?

My results provide a good rationale for future research into the effects of season of burn on the tree and grass component. A rigorous test of season of burn effects is required based on longer-term experiments and larger sample sizes. It is recommended that a 5-10 year or longer experimental burning programme be initiated to explore the potential of summer burns for tree control at a scale relevant for savanna range management. This should be coupled with a study of possible negative effects on the grass sward. In the HUP I recommend further investigation of occasional summer burns as a management practice where *D.cinerea* and/or *A.nilotica* are the species of concern.

3. What are the costs and benefits of different burning frequencies?

A similar experiment to the one described above should be conducted to investigate the effects of fire frequency. Several other studies have shown that tree height, cover and biomass are reduced with increasing fire frequency (e.g. Trapnell 1959; Trollope 1980;

Hoffman 1996). The notion of progressive weakening of the carbon reserves or exhaustion of bud banks could be tested in conjunction with such a study.

4. What role does accumulated carbon reserves play in tree recovery?

Rapid height growth in the pole stage is dependent on accumulation of several years of stored carbon in the roots but we know of no physiological studies of the phenomenon. The significance of root starch in post injury shoot recovery following burns in different seasons could shed more light on the underlying mechanism of different resprouting strategies. Is it possible for example to exhaust the starch reserves in *A.karoo* through repeated defoliation, and if so, could one simulate this through management techniques?

5. What is the physiology of the bud bank and what role does it play in tree recovery?

As an alternative to carbon reserves, one could investigate whether it is possible to kill a tree by exhausting the bud bank in a tree through repeated defoliation.

6. Do starch reserves in roots decline once trees have escaped the fire zone?

The failure of adult *A. karroo* and *A. nilotica* to sprout after decapitation might partly be as a result of loss of stored root reserves due to mobilisation for growth once plants have escaped the fire trap.

7. Is multi-stemmedness a key for distinguishing the gulliver vs non-gulliver life-histories in savanna trees?

Multi-stemmedness in adult trees may provide a shortcut for characterising species' life history types and should be further tested in other species and systems.

8. How do growth rates differ between savanna trees?

An understanding of tree height growth rates is the key for predicting the frequency of escape opportunities.

6.4 Conclusion

Savannas trees have very interesting life histories which are deserving of far more research attention. This is true not only from a management perspective but also from an evolutionary ecology perspective. Further research on which taxa moved out of forest into savannas environments and what traits enabled them to do so, are just some of the questions begging to be addressed.

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APPENDIX A

LOCATION AND PHYSICAL INFORMATION FOR EACH STUDY SITE

The site numbers correspond to those on the map in Figure 1.2, Chapter 1. A layer of shales and sandstones underlie the HUP with frequent dolerite intrusions. The basic soil types are fine textured sandy clays.

CLIPPING EXPERIMENT SITES

SITE NUMBER	SITE NAME	LATITUDE LONGITUDE	MEAN ANNUAL RAINFALL mm/yr	SOIL TYPE
1	Hilltop	28° 05' 15"S 32° 02' 40"E	990	Glenrosa D5 (20cm) (lithocutanic, orthic, small stones)
2	Isivivaneni north	28° 06' 02"S 32° 02' 30"E	980	Glenrosa D5 (20cm) (lithocutanic, orthic, small stones)
3	Isivivaneni south	28° 06' 15"S 32° 02' 40"E	980	Glenrosa D5 (20cm) (lithocutanic, orthic, small stones)
4	Masinda (arid site)	28° 18' 27"S 31° 57' 30"E	650	Shortlands D1 (orthic over red structure) 45% clay

CONTROLLED BURN SITES

SITE NUMBER	SITE NAME	LATITUDE LONGITUDE	MEAN ANNUAL RAINFALL mm/yr	SOIL TYPE
1	Gontshi winter	28° 01' 30" 32° 07' 28"	830	Glenrosa D4 40cm 45% clay
2	Magangeni winter	28° 02' 19" 32° 06' 11"	900	Glenrosa D5 10cm 55% clay
3	Zidonini winter	28° 08' 45" 32° 01' 24"	750	Glenrosa D5 (20cm) (lithocutanic, orthic, small stones)
4	Zinquimeni winter	28° 12' 24S 31° 57' 03E	690	Glenrosa D5 (20cm) (lithocutanic, orthic, small stones)
5	Zinquimeni summer	28° 12' 24S 31° 57' 00E	690	Glenrosa D5 (20cm) (lithocutanic, orthic, small stones)
6	Masendwini L	28° 12' 33N 31° 54' 42E	690	Glenrosa D5 (20cm) (lithocutanic, orthic)
7	Masendwini R	28° 12' 32N 31° 54' 45E	690	Glenrosa D5 (20cm) (lithocutanic, orthic)
8	Umfolozi summer	28° 14' 30S 31° 54' 46E	690	Glenrosa D4 (10cm)

SEASON CLIP SITE

SITE NUMBER	SITE NAME	LATITUDE LONGITUDE	MEAN ANNUAL RAINFALL mm/yr	SOIL TYPE
1	Mbembedwini	28° 12' 45S 31° 54' 38E	690	Glenrosa D5 (20cm) (lithocutanic)

APPENDIX B

TAXONOMY AND BOTANICAL DESCRIPTIONS OF THE FOUR STUDY SPECIES

Study Species

Acacia karroo, *A. nilotica*, *A. caffra* and *Dichrostachys cinerea* were chosen as the study species, since they are widespread within the Hluhluwe – Umfolozi Park and each of them presents a challenge to vegetation management. One of the key, yet occasionally overlooked, steps in research and management is the accurate identification of the organisms under study. In the case of savanna trees this is particularly important since varieties of one species may respond very differently under different conditions or disturbance regimes. The purpose of this appendix is therefore to provide details on the botanical descriptions and taxonomy of the four species and subspecies used for in study to avoid misapplication of the results and to assist with further research in this field.

Taxonomy and botanical descriptions

The genus *Acacia* Mill. is the largest (1250 species) and one of the most taxonomically complex in the sub-family Mimosoideae, and is the second largest in the family Fabaceae. There are 135 African species of which some 45 occur in South Africa. Short descriptions and taxonomy of the four main study species are given below. The genus *Dichrostachys* (DC) Wight & Arn. is a small genus in the sub-family Mimosoideae and is found mostly in tropical areas. Only one species occurs in South Africa.

Acacia karroo Hayne Arzney. Gebr. Gewachse 10:t.33 (1827) (Ross 1979; Pooley 1993)

Distribution: *A. karroo* is the most widespread tree in southern Africa, occurring over a range of environments from 200mm to over 1500mm annual rainfall, winter and summer rainfall and surviving all but the most severe frosts. Over a similar range of soil types it shows high regional variation (Ross 1979). Due to this variation, *A. karroo* has been the subject of great taxonomic debate. Some researchers have proposed that it is expanding its range (Barnes et al. 1996), particularly under disturbed ecological conditions into

former grassveld, into the surviving temperate forests of the eastern cape Province as well as the open savannas of the Northern and Eastern Provinces and KwaZulu Natal (Acocks 1988). In many areas of southern Africa the trees form dense, impenetrable thickets commonly referred to as bush encroachment. This has been attributed to bad grazing management in natural pastures (see Chapter 1 for more information) as well as more recently, to climate change (Bond pers com). *A.karoo* is currently listed on the National Department of Agriculture's encroaching species schedule.

Description: A shrub to 2m, often several stemmed, or a tree 25m high, crown typically somewhat rounded or flattened. Within *A.karoo* several "forms" are recognizable. In any research on *A.karoo* it is therefore important to accurately identify the "form" under study. Each of the different "forms" has a distinct morphology and most likely also a distinct set of responses to various disturbances. In the Hluhluwe-Umfolozi Park the "**spindle**" form of *Acacia karroo* is widespread in the landscape and it is highly efficient at invading and persisting in open savanna. The spindle form is endemic to Zululand, particularly the HUP. The "spindle" form is a slender, sparingly branched tree up to 6m high. In HUP however very few stands reach this height. Most typically trees dominate the landscape in the 1.5-3m size classes. The bark is typically reddish-brown, minutely flaking. Thorns are very short (3-7mm long) or absent. Leaves up to 55mm long with glaucous foliage, large flattened with discoid petiolar glands and a large gland at the junction of each or most pinnae pairs. Flowers are golden yellow balls. *A.nilotica* can be distinguished from *A.karoo* in HUP in its gulliver phase by its duller leaf colour, larger leaves and more slender habit. Mature trees however, have distinct growth forms.

General: *A.karoo* is a good fodder tree and browsed by stock and game. It is the preferred browse of black rhino in the Hluhluwe-Umfolozi Park.

***Acacia nilotica* (L.) Willd. ex Del., Fl. Aegypt. III. 79 (1813) (Ross 1979; Pooley 1993)**

Distribution: *A.nilotica* is the most widespread of the African Acacias, occurring in tropical and subtropical Africa and Asia, extending eastwards to India. It is also very variable with nine delimited sub-species, which are based mainly on differences in shape, size and

degree of pubescence of the pods. The subspecies in the Hluhluwe-Umfolozi Park is ***Acacia nilotica* subsp. *kraussiana*** (Benth.) Brenan, which occurs from Tanzania southwards to KwaZulu Natal, as well as in Angola and Namibia. *Acacia nilotica* subsp. *kraussiana* is also highly variable across its range.

Description: A small tree (3-6m), large trees often found in pure stands in the Hluhluwe-Umfolozi Park and elsewhere. Large trees are single stemmed with spreading, flattened crowns. Smaller trees or juveniles, usually have one main upright stem and several smaller branches from the base (see Chapter 2). The bark in adults is rough, fissured, and grey black. Branches and smaller trees have red-brown and finely flaking bark. Leaves are in clumps of 3-4 at nodes, twice compound (up to 40mm long); 3-9 pinna pairs, leaflets in 8-20 pairs, grey green to bright green, and with hairy stalks. Thorns are white, paired, straight, curving backwards in larger trees. Flowers are bright yellow balls. In the Hluhluwe-Umfolozi Park small trees are distinguished from *A.karoo* by their thicker stems, smaller leaves, and leaf colour being brighter green than *A.karoo*. This tree is an encroacher in some mesic grassland areas.

General: Leaves and new shoots are browsed by game.

Acacia caffra (Thunb.) Willd. Sp.Pl. 4: 1078 (1806) (Ross 1979; Pooley 1993)

Distribution: *A.caffra* is found in south-eastern Botswana, southern Mozambique, Swaziland, KwaZulu Natal, Northern Cape Province and north-western corner of South Africa. It occupies a diverse range of habitats and at its extremes the species look quite different (Ross 1979).

Description: Shrub or small tree to 3-14m high. In the Hluhluwe-Umfolozi Park it is nearly always multi-stemmed and never exceeds 4m in height. Young shoots and resprouts are heavily browsed. Flowers are more abundant in small trees relative to *A.karoo* and *A.nilotica* in the Hluhluwe-Umfolozi Park. Bark is rough and grey brown. Foliage is drooping and willow-like. Leaves are large, twice compound (60-230mm long) 7-24 pinna pairs, with fine leaflets, in 13-30 pairs (up to 7 x 1.1mm). Leaf stalks and rachis have prickles beneath. Prickles in pairs, recurved up to 9mm long. Flowers are creamy-white spikes, in cluster of 3-

5. Wood hard. A listed encroacher but does not encroach in the Hluhluwe-Umfolozi Park to any great extent.

General: Valuable fodder tree, browsed by game and favoured by black rhino.

***Dichrostachys cinerea* (L.) Wight Arn. (Mimosoideae) (Coates Palgrave 1984; Pooley 1993)**

Distribution: This species is widespread extending from Australia, through Burma and India and through many parts of tropical Africa. It is common at low altitudes, on a variety of soils in wooded grasslands. Over its range it is very variable. Taxonomically it has been divided into 10 subspecies and 11 varieties (Coates Palgrave 1984). Two subspecies occur in South Africa and both are found in the Hluhluwe-Umfolozi Park. These are *D.cinerea* subsp *africana* and *D.cinerea* subsp *nyassana*. The most common in Hluhluwe-Umfolozi Park and the one used in this study was ***Dichrostachys cinerea* subsp *nyassana***. Even within the Hluhluwe-Umfolozi Park and at Mkuze Game Reserve to the north, this species shows a great degree of morphological variation.

Description: Deciduous shrub or small tree (2-7m). A pronounced main stem with deeply grooved grey-black bark and a sparse flattish crown sets it apart from the sub-species *africana*. Its woody spine tipped twigs is distinguishing feature of the species. Leaves twice compound up to 25mm, up to 12 pinna pairs, olive green leaflets (11x3mm), glands on rachis conspicuous, long very thin at junction of bottom and top pairs. Flowers are 2 coloured spikes (pink above and yellow below when hanging in tree, although a white and yellow combination has been observed in Hluhluwe-Umfolozi Park). Can become very invasive in some areas and is a listed encroacher. It forms dense thickets in many parts of Hluhluwe-Umfolozi Park.

General: Very hard wood used for fence poles.

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